Social organization through self-organization

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SOCIAL ORGANIZATION THROUGH SELF-ORGANIZATION

Model and empirical data of macaques

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Contents

Chapter 1

General Introduction

Models of self-organization have shown that complex patterns of social behavior may emerge from simple behavioural rules and local interactions among individuals. This is usually accepted when explaining the intricate organization of social insects such as ants or termites (Camazine et al. 2001). However, when it comes to complex behavioural patterns of seemingly intelligent animals such as humans and non-human primates, simple explanations are usually discarded and sophisticated cognitive mechanisms favored (Shettleworth 2010). Recent studies, however, have shown that even in animal taxa with great cognitive sophistication complex patterns may emerge by self-organization and cognitively simple behavioural rules (Shettleworth 2010; Hemelrijk & Bolhuis 2011; van der Vaart et al. 2012). For instance, even in humans, complex patterns such as segregation of races (Schelling 1978), financial markets (Farmer et al. 2005), and crow dynamics (Moussaid et al. 2011) may be explained in this way. Thus, whether sophisticated cognition is absolutely necessary for the display of complex social behavior is a point of view shared by some scientist but not by others. For instance, Barret and co-authors (2007), Henzi and Barret (Barrett & Henzi 2005) argue that in societies of primates rather than cognitive sophistication, simple rules of thumb may suffice to explain the complex social behavior displayed by individuals. During my PhD I used individual-based models based on simple cognitive rules and local interactions to study the complex social organization of primates, especially macaques. My main goal was to develop a computational null-model of primate social behaviour that could be used as a tool to understand complex social behaviour of real primates, as has been suggested by several primatologists (te Boekhorst & Hogeweg 1994; Hemelrijk 2002; Aureli et al. 2008). I started by extending a previous individual-based model of grouping and aggression, the Dom-World model (Hemelrijk 1999a). The extension consisted of the addition of grooming behavior. I chose DomWorld, because this model had already reproduced many of the patterns of aggression, dominance and spatial structure observed in despotic and egalitarian societies of macaques (Hemelrijk 1999a; Hemelrijk 2004; Hemelrijk et al. 2008a; Hemelrijk 2013). In the new model, called GrooFiWorld (Grooming and Fighting World), individuals tend to group and when close-by they fight if their chance of winning is

high, otherwise they consider grooming, especially when anxious. With these simple behavioural rules I was able to explain and predict many complex behavioural patterns of aggression and affiliation and their differences between egalitarian and despotic societies of primates, especially macaques.

In the following subsections I first describe the genus of macaques (*Macaca sp*), its basic features and the classification of macaque species in despotic and egalitarian. Second, I discuss grooming, its functions and its distribution among individuals in macaque societies. Third, I briefly discuss the two most prominent theories on the evolution of brain size and studies on primate cognition. I end up with a brief overview of this thesis.

Macaque societies

The genus of *Macaca* is a monophyletic group which comprises 22 species (Thierry 2007). The genus has the broadest geographical range and the widest habitat diversity (from tropical to temperate regions) known in non-human primates, both within and between species (Thierry et al. 2000). They form multi-male multi-female groups with adult sex ratio biased towards females. Whereas most males disperse from their natal groups, most females remain in their groups forming matrilineals of kin-related individuals. Thus, the dominance ranks of males vary over their lifetimes in contrast to that of females which remain quite stable. Besides these basic shared features, macaques display a broad interspecific variation regarding patterns of aggression, affiliation, reconciliation, dominance, nepotism, socialization, and temperament (Thierry et al. 2000; Thierry 2007).

Macaque societies can be broadly categorized in two different types, despotic and egalitarian. Whereas in despotic societies aggression is fierce (e.g. slaps, bites), in egalitarian societies it is mild (e.g. threats and chases) (Thierry et al. 2004). Several different behavioral traits seem to be correlated with intensity of aggression. For instance, in despotic societies aggression is usually unidirectional, dominance hierarchy is steep, affiliative interactions are usually among kin, and reconciliation is infrequent and kin-biased. In egalitarian societies on the other hand, aggression is often bidirectional (i.e. counter-aggression is common), the

dominance hierarchy is shallow, affiliative interactions are distributed among all members of the group (kin or non-kin), and reconciliation is frequent (Thierry et al. 2008). Based on interspecific variation in social traits, Thierry (2000) proposed a 4-grade scale of social organization for macaques. Species in grade 1 (e.g. Japanese and rhesus macaques) are characterized by being extremely despotic and species in grade 4 (Tonkean, Moor and Crested macaque) by being extremely egalitarian. Other macaque species are place intermediately depending on the social structure they resemble most. For instance, long-tailed and pigtail macaques resemble more despotic societies and thus they are placed in grade 2. On the other hand, stumptail, Barbary, lion-tailed, and bonnet macaques are placed in grade 3 because of their resemblance to egalitarian societies (Thierry 2000). In addition, macaque species seem to cluster in the phylogenetic tree according to the type of society to which they belong. Thus, that despotic species are phylogenetically closer among themselves than egalitarian species suggests that intensity of aggression may be a genetically inherited trait (Thierry 2004; Thierry 2007).

Grooming

Grooming is one of the most conspicuous behaviours in primate societies. It comprises the brushing and picking at the hairs of the fur. Two types of grooming are distinguished: auto or self-grooming and social or allo-grooming, i.e. grooming directed to another individual. Initially, it was argued that allo-grooming (grooming hereafter) served a purely hygienic function (Barton 1985; Saunders 1987); however, nowadays it is assumed that grooming also serves an important function for the social life of the individual (Goosen 1987). Besides cleaning of the fur, two other functions are attributed to grooming, a) physiological functions such as reduction of tension and b) social functions such as establishing and maintenance of social relationships.

Evidence in support of grooming as a tension reduction mechanism is compelling. For instance, Boccia (1987) monitored heart rate in a female pigtail monkey and found that receipt of grooming reduced tension physiologically. Schino et al. (1988) used displacements activities (auto-grooming, yawning, body shake

and scratching) as a measure for the level of tension and found a negative correlation between level of tension and grooming received. In addition, several studies have shown that grooming stimulates the release of β-endorphins, an endogenous opioid peptide neurotransmitter with analgesic effects (Keverne et al. 1989), and that administration of exogenous opiates or opiate antagonists to monkeys, reduces or increases the frequency of grooming respectively (Meller et al. 1980; Fabre-Nys et al. 1982; Schino & Troisi 1992; Martel et al. 1995; Graves et al. 2002). Finally, a recent study in Barbary macaques showed that not only receiving grooming but also actively grooming reduces tension in an individual (Shutt et al. 2007)

Besides its physiological function, several other functions are attributed to grooming in the social domain. For instance, it has been suggested that individuals use grooming to establish and maintain social bonds, i.e. 'friendships' (Silk 2002a; Massen et al. 2010) and as a currency to exchange for itself or other commodities such as support in fights, food, tolerance, mates, etc. (Seyfarth 1977; Henzi & Barrett 1999). Further, grooming between former opponents immediately after the fight is interpreted as a mean to repair and preserve social relationships. This behaviour, called reconciliation, occurs in many primate species and it happens more often between valuable partners (i.e. individuals that groom the most) than among non-valuable ones (Aureli et al. 2002; Silk 2002b). Similarly, grooming between a by-stander and the former victim or the former aggressor immediately after the conflict is over is interpreted as if the by-stander tries to 'console' or 'appease' respectively, the former opponent of the fight(Fraser et al. 2009),

The way grooming is distributed among individuals within in a primate society seems to depend on the type of society, egalitarian or despotic. Whereas in both types of societies grooming is reciprocated, in despotic societies grooming is also directed up the dominance hierarchy and occurs frequently among individuals of similar rank. According to biological market theory, this is due to a difference in the exchange rate of commodities between the two dominant styles. In despotic societies, characterized by steep dominance hierarchies, high ranking individuals are considered more valuable at providing commodities than high ranking

individuals in egalitarian societies, where dominance hierarchies are shallow (Henzi & Barrett 1999). Thus, the fact that only in despotic societies individuals direct grooming up the dominance hierarchy is interpreted as if individuals in these societies attempt to interchange grooming for commodities with high ranking individuals. However, due to competition to groom high ranking individuals, individuals end up grooming others of similar rank (Seyfarth 1977).

Primate cognition

Two hypotheses have been put forward to explain the fitness advantages primates may gain from having relatively large brains. The first suggests the physical environment as the main selective force for larger brains. Learning and recalling when and where food might be available, how to use tools to extract food, or how to navigate visually through a three-dimensional arboreal world, may have produced larger brains (Harvey et al. 1980). The second hypothesis states that, instead of the physical environment, group living and local competition for resources selected for social manipulation to achieve individual benefits at the expense of others (Byrne & Whiten 1997; Dunbar 1998). Social manipulation, thus, would be favored as a trait and because this selective pressure is applied to all the individuals in the group, an evolutionary arms-race is set up leading to increases in intelligence (Byrne & Whiten 1997). The latter hypothesis is the most well accepted and it is known as the 'Machiavellian intelligence hypothesis' (Byrne & Whiten 1988) or the social brain hypothesis (Dunbar 1998).

Evidence in favour of the social brain hypothesis comes mainly from correlational studies between brain size and different indices of social complexity, mainly group size. For instance, size of the group, size of the grooming clique, social skills in mating strategies, tactical deception, and social play seem to positively correlate with neocortex volume in primates (Dunbar 2003; Shultz & Dunbar 2010). Besides, seemingly complex social behaviours such as coalition formation, reconciliation, post-conflict affiliation between a former opponent and a bystander, and reciprocation and interchange of grooming and support are the typical examples used to indicate high cognitive abilities in primates. For instance, it is

assumed that to recruit coalition partners, individuals not only use physical traits (e.g. body size) but also information about third-party relationships (Cheney & Seyfarth 1999; Silk 1999; Bergman et al. 2003; Perry et al. 2004; Schino 2007). To reconcile individuals need a memory of the former opponent and a conciliatory disposition (de Waal & Yoshihara 1983); and to reconcile with valuable partners an assessment of the quality of past interactions with other individuals is also needed (Silk 2002b). As to post-conflict affiliation between a former opponent and a bystander, special emphasis is put on 'consolation' (affiliation directed to the victim), which is interpreted as expression of cognitive empathy (i.e. an understanding of the emotional state of others) (Preston & de Waal 2002). In addition, according to the biological market theory, primates are viewed as traders that engage in an exchange of mutually beneficial commodities. Thus, individuals should be able to select the appropriate social partner offering them the best value (Henzi et al. 2003; Barrett et al. 2007); and, to avoid cheating, keep records of what they have given and received (de Waal & Luttrell 1988). Since all these behaviours are thought essential in maintaining the internal structure of primate social groups and because group and grooming clique size correlate with neocortex ratio, it is assumed that cognitive complexity was selected to track many relationships through time and to make decisions such as with whom to groom and reconcile; whom to support, attack, console or appease; when to engage in a coalition or alliance, and when to hold back; long term strategies that may be the product of high cognitive abilities (Barrett & Henzi 2005; Barrett et al. 2007).

However, whether a big brain size corresponds to a high degree of complex behaviour or cognitive abilities is still controversial. For instance, a recent review of correlational studies between brain size and complex behaviour has pointed out several problems such as the omission of important ecological variables (e.g. diet and developmental mode) in the correlational analyses and the difficulty to measure complex behaviour (Healy & Rowe 2007). Furthermore, brain size per se may not be critical of higher cognitive abilities, instead modularity and interconnectivity may be more important (Chittka & Niven 2009; Avargues-Weber et al. 2013; Avarguès-Weber & Giurfa 2013). In addition, nowadays it is known that

monkeys lack an understanding of thoughts, beliefs, and desires of others or their own (Barrett & Henzi 2005), are not able to plan for future (Roberts 2002; Suddendorf & Corballis 2007), remember when an event happened (Hampton et al. 2005), and engage in a truly causal and analogical reason (Thompson & Oden 2000). Recent studies on systematic comparisons of cognitive skills show that even though monkeys, apes, and human toddlers may have similar competencies in the physical domain, human children excelled in socio-cognitive tasks such as attention sharing, cooperation and mental state attribution (Herrmann et al. 2007; Amici et al. 2010; Schmitt et al. 2012).

Overview of this thesis

If high cognitive mechanisms are unlikely to be behind the complex behavioural patterns we observe in monkeys societies; then, what kind of mechanisms are? The goal of my PhD was to search for alternative, more parsimonious mechanisms that may answer this question. In order to do so, I extended a previous individual-based computer model of grouping and aggression, the Dom-World model. The extension consisted of the addition of grooming behaviour to which the only function given was that of a tension reduction mechanism. The main part of this thesis starts in **Chapter 2** where I explored the consequences of adding grooming behaviour to the Dom-World model. In the new model called GrooFiWorld (Grooming and Fighting world), I looked at the distribution of grooming among individuals and their differences between high and low intensity of aggression. I validated the model by comparing the affiliative patterns that emerged with those described in empirical data of despotic and egalitarian societies of macaques. The model provided us with new explanations as regards the distribution of grooming in real macaque (primate) societies. Surprisingly, we observed coalitions in the model. Coalitions emerge when incidentally, after a fight between two individuals (A and B), a third individual (C) attacks one of the two combatants (e.g. A). Here, C supports B and opposes A. In **chapter 3** I investigated whether patterns of coalition, such as reciprocation of support and the interchange between support given and grooming received and active grooming for support received, emerged through self-organization and

simple behavioural rules. Besides confirming the emergence of the coalition patterns already described in primate literature, the GrooFiWorld model generated novel predictions as regards patterns of opposition (also called contra-support). For instance, the model predicted that when females intervene in fights, they will oppose more often those females i) that they attack more during dyadic fights and ii) from whom they receive more grooming. In **chapter 4** we tested and confirmed these novel predictions in empirical data from three different species of macaques: bonnet (*Macaca radiata*), Assamese (*Macaca assamensis*), and rhesus (*Macaca mulatta*) macaques. In **chapter 5** I studied in the model and in empirical data of Tonkean macaques (*Macaca tonkeana*) post-conflict affiliation between a former opponent and a by-stander of a fight. For doing so, I simulated the group of Tonkean macaques in the GrooFiWorld model by setting the parameters of the model to the same intensity of aggression, group size, sex ratio, female dominance, steepness of the hierarchy and ratio of grooming to aggression as in the group of Tonkean macaques. We found evidence of post-conflict affiliation between former opponents and bystanders in both the model and empirical data. Moreover, the frequency and distribution of post-conflict affiliation received and solicited appeared to be similar in the empirical data and the model. The model suggested two mechanisms as causes for the emergence of these post-conflict affiliations: social facilitation and anxiety reduction. In **chapter 6**, I extended the model further to investigate the effects of 'friendships' on the patterns of reciprocation and interchange of grooming and support. In the new model called 'FriendsWorld', individuals follow their 'friends', i.e. those with whom they affiliate the most. This mechanism was motivated by the assumption that grooming may produce a positive emotion (i.e. relaxation) in the groomee and groomer. Since this emotion occurs more frequently with some than with others, individuals may learn to associate a positive emotion with specific partners (i.e. their friends), and try to stay close to them. Compared to GrooFiWorld, we showed that in FriendsWorld the mere act of following friends causes individuals to interact more often with friends than with non-friends, and as a consequence the patterns of reciprocation and interchange become significantly stronger. Finally, in **chapter 7** I discuss several

topics that could not be included as chapters in this thesis. Namely, I discuss the results obtained when reconciliation is measured with the time-rule method, the decrease in reconciliation when controlling for proximity between former opponents, the implementation of coalition rules in the GrooFiWorld model, and the results of the model in an evolutionary context.

Chapter 2

Emergent Patterns of Social Affiliation in Primates, a Model

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Abstract

Many patterns of affiliative behaviour have been described for primates. For instance, reciprocation and exchange of grooming, grooming others of similar rank, reconciliation of fights, and preferential reconciliation with more valuable partners. For these patterns several functions and underlying cognitive processes have been suggested. It is, however, difficult to imagine how animals may combine these diverse considerations in their mind. Although the co-variation hypothesis, by limiting the social possibilities an individual has, constrains the number of cognitive considerations an individual has to take, it does not present an integrated theory of affiliative patterns either. In the present paper, after surveying patterns of affiliation in egalitarian and despotic macaques, we use an individual-based model with a high potential for self-organisation as a starting point for such an integrative approach. In our model, called GrooFiWorld, individuals group and, upon meeting each other, may perform a dominance interaction of which the outcomes of winning and losing are self-reinforcing. Besides, if individuals think they will be defeated, they consider grooming others. Here, the greater their anxiety is, the greater their 'motivation' to groom others. Our model generates patterns similar to many affiliative patterns of empirical data. By merely increasing the intensity of aggression, affiliative patterns in the model change from those resembling egalitarian macaques to those resembling despotic ones. Our model produces such patterns without assuming in the mind of the individual the specific cognitive processes that are usually thought to underlie these patterns (such as recordkeeping of the acts given and received, a tendency to exchange, memory of the former fight, selective attraction to the former opponent, and estimation of the value of a relationship). Our model can be used as a null model to increase our understanding of affiliative behaviour among primates, in particular macaques.

Introduction

Patterns of affiliative behaviour have long puzzled primatologists. One of the most frequent behavioural acts is grooming. It has been explained as serving several functions, such as cleaning the fur (Barton 1985), reducing anxiety, tension and stress (Goosen 1987), social bonding (Dunbar 1988), repairing relationships (Arnold & Aureli 2006) and social reciprocation and exchange (Henzi et al. 2003). As regards the mechanisms of exchange, individuals have been supposed to direct grooming up the hierarchy in order to receive more effective support in return, and due to competition for partners of high rank they may end up grooming others of similar rank (Seyfarth 1977). Besides, they were also supposed to groom others of similar rank, because individuals of similar rank have similar needs (de Waal & Luttrell 1986). Grooming between two former opponents immediately after a fight has been interpreted to function as a means to repair the relationship or 'reconcile', because it occurred significantly earlier after a fight than otherwise in matching control periods the next day. Besides, individuals appeared to reconcile in particular with those partners that appeared more valuable to them, the so-called 'valuable-relationship hypothesis' (Aureli et al. 2002).

To complicate matters, the degree of exchange and reciprocation (Barrett et al. 1999) appeared to differ between egalitarian and despotic species. Applying market theory (Nöe & Hammerstein 1994; Nöe & Hammerstein 1995), this was explained by assuming that the exchange rate of services differed between the two competitive regimes (Barrett et al. 1999). Further, the co-variation hypothesis explained the lower conciliatory tendency in despotic societies by the greater danger involved in reconciliation in these species (Thierry 2004).

Many specific cognitive considerations have been suggested to underlie these affiliative patterns. For instance, as regards reciprocity and exchange, the individuals are supposed to keep records of the acts of grooming and tune them to frequencies of receipt of being groomed or another act, such as support (de Waal & Luttrell 1988), and to use their knowledge of the ranks of others to obtain more effective support (Seyfarth 1977; Seyfarth 1981). Besides, individuals have been supposed to be attracted to others of higher rank (Seyfarth 1977) and to others of

similar rank (de Waal & Luttrell 1986). The supposed cognition underlying reconciliation consists of the ability to remember the former opponent and of selective attraction to the former opponent or a conciliatory disposition (de Waal & van Roosmalen 1979; de Waal & Yoshihara 1983). As to their inclination particularly to reconcile fights with opponents that are of greater value to them, the so-called 'valuable-relationship hypothesis' (Castles et al. 1996; Schino et al. 1998; Call et al. 1999; Arnold & Barton 2001; Aureli et al. 2002; Cooper et al. 2005; Majolo et al. 2005; Koski et al. 2007), three key components are supposed to influence the quality of a relationship, namely its security, its value, and the compatibility of both partners (Cords & Aureli 2000; Aureli et al. 2002). According to Silk (2002b) this implies that assessing the value of a relationship over the long-term requires cognitive sophistication, because it asks for a precise memory of what happened in the past and for a correct evaluation of the relationship in the long run.

These theories of affiliation pose several problems. First, evidence for each of these theories is not conclusive (Hemelrijk & Ek 1991; Matheson & Bernstein 2000; Henzi et al. 2003; Schino et al. 2003; Manson et al. 2004; Gumert & Ho 2008). Second, from a scientific perspective, these numerous different theories for specific patterns of affiliation (such as exchange and reconciliation) must be integrated in some way. Third, the use of grooming as a 'currency of exchange' is dangerously anthropomorphic according to us and others (Hemelrijk 1996b; Silk 2002b; Barrett et al. 2007). As a more parsimonious alternative, we suggest to follow a more distributed approach based on local interactions and rules of thumb (Hemelrijk 2002; Hemelrijk 2004; Hemelrijk 2005; Barrett et al. 2007; Aureli et al. 2008). Fourth, even though primates are obviously intelligent (Tomasello & Call 1997; Cheney & Seyfarth 2007) it seems much to ask of primates to combine intentionally all these rational considerations in the distribution of their affiliative behaviour (e.g. to consider what incidence of grooming was used in exchange for something, and what for reconciliation or maintenance and development of social bonds). Fifth, often simple rules suffice to cause many of the observed patterns and herewith an integrative theory (Camazine et al. 2001; Hemelrijk 2002). Therefore fewer cognitive processes may suffice as shown for instance in a model for dominance

style (Hemelrijk 1996b; Hemelrijk 1999a). A similar integrative approach based on fewer cognitive processes is also suggested by the co-variation hypothesis (or theory of social epigenesis). In this theory part of the behavioural acts is supposed to be forced by constraints due to the specifics of the social structure (Thierry 2004).

For these reasons, we use in the present paper a computer model to develop an integrative approach to patterns of social affiliation in primates. We first precede this by a survey of the precise patterns of dominance style and affiliation found in the literature. In the model, we assume very little cognitive deliberations by the individuals to groom others: Individuals merely groom others out of fear of being defeated and to reduce their own anxiety. Individuals do not intend to reconcile fights nor to exchange or reciprocate grooming. Our model is an extension of our earlier model of grouping and competition, called DomWorld (Hemelrijk 2000a; Hemelrijk & Wantia 2005). We choose DomWorld, because it has reproduced many of the patterns of aggression, dominance and spatial structure that have been observed in despotic and egalitarian societies of primates, in particular of macaques. These have arisen merely as a side effect of local rules for grouping and competition through the feedback between hierarchical development and spatial-social structure with dominants in the centre and subordinates at the periphery (Hogeweg 1988; Hemelrijk 1999a; Hemelrijk 1999b; Hemelrijk 2005; Hemelrijk et al. 2008a). Note that the hierarchy develops via self-reinforcing effects of victory and defeat, which have been described for many species including primates (Mendoza & Barchas 1983; Barchas & Mendoza 1984; Eaton 1984; Hsu et al. 2006; Hemelrijk et al. 2008a). Through these self-reinforcing effects, occasional victories of low ranking individuals may lead to rank reversals. This is important, because dominance hierarchies in empirical data are not entirely stable (Samuels et al. 1984; Rhine et al. 1989; Sapolsky 1992; Berman et al. 2004; Singh & Krishna 2006).

Interactions in our new model, called GrooFiWorld (a contraction of groom and fight), are extended with the option to groom. When individuals meet each

other at close proximity, they will consider whether to groom, to fight or to rest. As to the order of what to do first, we are led by four observations: first, those on baboons by Kummer (1974) who inform us that upon their first encounter individuals first fight and later groom; second, by the empirical finding that an individual builds up anxiety (as indicated by the increased heart rate) when approaching an opponent by whom it may be defeated (rhesus monkeys, Aureli et al. 1999); third, that anxiety increases after a fight as is indicated by the increase in frequency of scratching and heart rate in both opponents (Aureli et al. 1989; Aureli & van Schaik 1991; Aureli 1992; Aureli 1997; Castles & Whiten 1998; Das et al. 1998; Silk 2002b; Cooper et al. 2007); fourth, that anxiety may subsequently be reduced (in many species) by the receipt of affiliative behaviour as indicated by the reduced heart rate and the rate of self-directed behaviour (Aureli & van Schaik 1991; Castles & Whiten 1998; Das et al. 1998; Aureli et al. 1999) and to a lesser degree by active grooming (Shutt et al. 2007). Furthermore, our model is informed by empirical studies on grooming and opiate administration which indicate that not being groomed for some length of time reduces the concentration of endorphins and increases the motivation to be groomed, and that grooming increases the level of endorphins in the brain and reduces the motivation to groom (Meller et al. 1980; Fabre-Nys et al. 1982; Keverne et al. 1989; Schino & Troisi 1992; Martel et al. 1995; Graves et al. 2002).

In sum upon encountering someone else, an individual in our model first deliberates whether or not to attack. This decision depends on the risks involved (whereby risk concerns the chance of losing a fight), as is the case among primates (Popp & DeVore 1979), and as in our earlier model: a fight is only initiated when the individual expects to win (Hemelrijk 1998; Hemelrijk 1999a). If defeat is expected, its fear of losing makes the individual consider grooming the other. Its decision whether or not to groom depends on its degree of anxiety: an individual that is more anxious is more inclined to groom (instead of resting close by). After being groomed by another and (a little less) after actively grooming another, its anxiety and therefore its tendency to groom diminishes. Its anxiety also increases

after a fight and after a period of not having been involved in grooming. Note that we do not distinguish between anxiety, tension or stress.

In order to compare the patterns of affiliative behaviour in our model with those in real primates, we used the same statistical measures as applied in empirical data and we confined ourselves to macaques for two reasons. First, because their social behaviour has been studied extensively and shown to differ in interesting ways between the typical egalitarian and despotic societies (Thierry et al. 2004; Thierry et al. 2008). Second, because in our earlier model, DomWorld, patterns of dominance and aggressive interaction were remarkably similar to those of macaques (Hemelrijk 1999a; Hemelrijk et al. 2008a). Since GrooFiWorld is an extension of this model, we assume it to also be suitable for comparing to macaques.

The paper is organized as follows. First, we summarise the literature on the common patterns of affiliative behaviour in females of egalitarian and despotic species of macaques (Table 1). Second, we tune the percentage of grooming time and the unexpectedly emerging percentage of reconciliation to empirical data for despotic societies. Third, by varying the intensity of aggression we show the emergence of all these common patterns of affiliation and their differences between typical egalitarian and despotic macaque species in GrooFiWorld. Fourth, in order to understand how these patterns emerge, we remove different assumptions in turn, such as the self-reinforcing effects of victory and defeat and effects of spatial proximity. Fifth, the explanation of the causation of these patterns in the model leads to new hypotheses about the interconnection between other traits which we confirm in the model. Part of these predicted patterns appear also to be found in empirical data described by scientists in other contexts. Other patterns still need to be tested empirically. Since for all patterns empirical data are insufficient, we list them together in Table 2 so that the relevance of our model to empirical data may be tested in the future.

Methods

The model

The model is individual-oriented and event-driven (Judson 1994). It has been written in C++, as an extension of a previous model of grouping and competition, called *Dom*-World (Hemelrijk 1999a; Hemelrijk 2000b; Hemelrijk et al. 2003; Hemelrijk & Wantia 2005) which has been reimplemented in C++ by Hanno Hildenbrandt. The extension consists of the addition of grooming behaviour (for default parameters see Table 3). Therefore, we call it 'GrooFiWorld'. The individuals are provided with three tendencies: 1) to group, 2) to perform dominance interactions and 3) to display affiliative behaviour. Why individuals actually group (whether to avoid predators or because resources are clumped) is not specified and irrelevant to the model. The same holds for dominance interactions which may reflect competition for resources such as food and mates, but these resources are not explicitly specified in the model. Individuals groom to reduce *Anxiety*, as suggested for real primates (Meller et al. 1980; Fabre-Nys et al. 1982; Boccia 1987; Keverne et al. 1989; Schino & Troisi 1992; Martel et al. 1995; Graves et al. 2002; Sannen et al. 2004).

GrooFiWorld consists of a 'world' (without borders) containing its interacting individuals. The space of the 'world' is continuous, i.e. individuals are free to move in any direction. Individuals have a certain angle of vision (*VisionAngle*) and a maximum distance of perception (*MaxView*). At the start of each run they occupy random locations within a predefined circumference, *InitRadius,* which is the product of an arbitrary constant times the number of individuals.

Activities of individuals are regulated by a timing regime in which each individual receives a random waiting time from a uniform distribution and the individual with the shortest waiting time is activated first. This regime is combined with a biologically plausible timing regime reflecting a kind of social facilitation (e.g., see Galef 1988) in which the waiting time of an individual is shortened when a dominance interaction occurs close by (within the individual's *NearView*).

Species	*Macaca mulatta*	*Macaca fuscata*	*Macaca assamensis*	*Macaca thibetana*	*Macaca nemestrina*	*Macaca fascicularis*	*Macaca sylvanus*	*Macaca radiata*	*Macaca arctoides*	*Macaca silenus*	*Macaca nigra*	*Macaca tonkeana*
Dominance style	D[1]	D[1]	D[1]	D[2]	D[3]	D[1]	E[1]	E[1]	E[1]	E[1*]	E[1]	E[1]
Unidirectionality aggression[1]	True	True	True	True	True	True	Not true	Not true	Not true	Not true	Not true	Not true
Frequency of aggression	Low[5]	NA	NA	NA	NA	NA	NA	NA	High[5]	NA	NA	High[6]
Interindividual distance	High[5]	NA	NA	NA	NA	NA	NA	NA	Low[5]	NA	NA	Low[6]
Centrality of dominants	NA	True[4]	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Conciliatory tendency	~7%[1]	~10%[1]	~11%[7]	~6%[8]	~32%[9]	~18%[1]	~20%[1]	~29%[10]	~35%[11]	~70%[1]	~50%[1]	~50%[1]
Grooming reciprocation	True[12]	True[12]	NA	NA	NA	True[12]	True[12]	True[12]	True[12]	NA	NA	True[6]
Grooming up the hierarchy	True[13,14]	True[13,15,16]	True[17]	NA	NA	True[13,14]	NA	NA	Not true[18]	NA	NA	Not true[6]
Grooming partners of similar rank	True[13,14]	True[13,16]	NA	NA	NA	True[13,14]	NA	NA	Not true[18]	NA	NA	Not true[6,18]
Reconciliation with valuable partners	NA	True[19]	True[20]	True[8]	True[9]	True[21]	NA	NA	True[11]	NA	NA	NA

Table 1. Dominance style and affiliative patterns for different species of macaques, D = despotic, E = egalitarian.* indicates that there is debate about the classification of the dominance style of this species. [1] (Thierry 2004); [2] (Berman et al. 2004); [3] (Cooper & Bernstein 2008); [4] (Itani 1954; Imanishi 1960; Yamada 1966); [5] (Boccia et al. 1989; de Waal & Luttrell 1989); [6] (Schino et al. 1988; Thierry et al. 1990); [7] (Cooper & Bernstein 2002); [8] (Berman et al. 2006); [9] (Castles et al. 1996; Schino et al. 2007); [10] (Cooper et al. 2007); [11] (Call et al. 1999; Gumert 2007; Gumert & Ho 2008); [12] (Schino & Aureli 2008a); [13] (Schino 2001); [14] (de Waal & Luttrell 1986)[7]; [15] (Schino et al. 2003); [16] (Nakamichi & Shizawa 2003); [17] (Cooper & Bernstein 2008); [18] (Butovskaya 2004); [19] (Kutsukake & Castles 2001; Majolo et al. 2005) ; [20] (Cooper et al. 2005); [21] (Cords & Thurnheer 1993).

Model-based hypotheses	Empirical Data
A) In general:	
1) Positive correlation between proximity and grooming	(de Waal & Luttrell 1989; Thierry et al. 1990; Singh & Krishna 2006)
2) No correlation between frequency of grooming by an individual and its rank	pro: (Seyfarth 1976; Seyfarth 1980) contra: (Singh & Krishna 2006).
3) Positive correlation between grooming up the hierarchy and the gradient of the hierarchy	(Schino & Aureli 2008b)
4) Positive association between grooming others of similar rank and spatial centrality of dominants	(de Waal & Luttrell 1986)
5) Positive correlation between % time grooming and % reconciliation in group	Not available
6) Positive correlation between % interactions spent in grooming and % reconciliation in group	Not available
7) Negative association between spatial rigidity and conciliatory tendency	Not available
B) In despotic species:	
1) Conciliatory tendency directed up the hierarchy	(Silk et al. 1996)
C) In despotic species (compared to egalitarian ones):	
1) The gradient of the hierarchy is steeper	(van Schaik 1989; Barrett et al. 1999; Henzi & Barrett 1999)
2) Higher ranking individuals are more often aggressive	Not available
3) Higher ranking individuals receive less aggression	Not available
4) Lower ranking individuals lose more fights	Not available
5) Percentage of fighting is lower	(de Waal & Luttrell 1989)
6) Distance among group members is larger	(de Waal & Luttrell 1989; Thierry 1990; Arnold & Whiten 2001; Majolo et al. 2009)
7) The spatial structure (with dominants in the centre) is stronger	Not available
8) The time spent grooming is lower	(de Waal & Luttrell 1989)
9) Percentage of interactions spent in grooming is lower	Not available
10) The diversity of neighbours is lower	Not available
11) Stronger association between spatial proximity of partner and conciliatory tendency	Not available
12) Negative correlation between dominance and anxiety is stronger	Not available
13) The percentage with which females groom males is lower	Not available

Table 2. List of model based hypotheses that emerge in the model

Parameter	Description	Females	Males
General Parameters			
Total Individuals	Total number of individuals	12	
Sex ratio (at high aggression intensity)	Number of males and females	10	2
Sex ratio (at low aggression intensity)	Number of males and females	8	4
InitRadius	Predefined space at start of simulation	1.7*# Inds	1.7*# Inds
Grouping Parameters			
Perspace	Close encounter distance	8	8
Nearview	Medium distance	24	24
MaxView	Maximal viewing distance	50	50
SearchAngle	Turning angle to find others	90°	90°
VisionAngle	Angle of field of view	120°	120°
Dominance Parameters			
InitDom	Initial Dom value	16	32
RiskSens	Number of 'mental battles'	2	2
StepDom (high aggression intensity)	Scaling factor for aggression intensity	0.8	1
StepDom(low aggression intensity)	Scaling factor for aggression intensity	0.08	0.1
Fleeing Dist	After loosing a fight	2	2
Grooming Parameters			
InitAnx	Initial anxiety value	0.5	0.5
AnxInc	Increase in anxiety after every activation	1%	1%
AnxDcrGree	Decrease in anxiety in groomee	0.15	0.15
AnxDcrGrmr	Decrease in anxiety in groomer	0.1	0.1
AnxIncFight	Increase in anxiety after fighting	0.1	0.1

Table 3. Default parameter values in 'GrooFiWorld'.

Grouping rules

Whenever an individual does not see another one close by (within its personal space, *PersSpace*), grouping rules come into effect. The individual starts looking for others at greater and greater distances (*NearView* and *MaxView*). If, even then, no one else is in sight, it turns over a *SearchAngle* in order to scan for others. In this way individuals tend to remain in a group (Figure 1 and Table 3). If, however, an

individual spots another one close by, within its personal space (*PersSpace*), a social interaction may take place.

Interactions

Upon encountering someone else the individual first deliberates whether or not it will perform a dominance interaction on the basis of the risk of losing the fight (following the so-called 'risk-sensitive attack strategy', Hemelrijk 2000a). Only if it expects to be defeated, it will consider grooming. In real primates, motivation to groom depends on opiate concentrations as well as on other physiological conditions such as stress levels, and we have coded these factors together as *Anxiety* (Fabre-Nys et al. 1982; Keverne et al. 1989; Martel et al. 1994; Martel et al. 1995; Graves et al. 2002) (Figure 1). Thus, in GrooFiWorld, first, the more anxious an individual is the more likely it is to groom (instead of resting close by); second, after being groomed and (a little less) after actively grooming another, an individual's anxiety and thus its tendency to groom declines; third, after not having been involved in grooming for some time an individual's anxiety builds up again; and fourth, an individual's anxiety grows after a fight. Thus anxiety reflects the psychological and physiological state of an individual.

Dominance rules

Dominance interactions are modelled as before (Hogeweg 1988; Hemelrijk 1999a) and they are an extension of the DoDom rules of Hogeweg (1988). First, an individual *i* estimates whether it will win on the basis of a 'mental battle' (Equation 1). It may do so once (Hemelrijk 1998) or repeatedly depending on its degree of sensitivity to risks (*RiskSens* Table 3 and Parameters and Experimental Setup). Higher values of *RiskSens* indicate that individuals need to win several mental fights before starting an actual interaction. Here, individuals *i* and *j* observe each other's capacity of winning, i.e. their dominance values Dom_i and Dom_j. The probability of winning for individual *i* is greater if it is higher in rank, and this is proportional to the *Dom*-value of individual *i* relative to that of its opponent *j* (Equation 1). It expects to be victorious if its relative dominance value is greater than a random value drawn from a uniform distribution between zero and one. If this is the case, a dominance interaction takes place. During the actual dominance interaction, the

individual *i* compares its relative dominance value again with another value randomly drawn and if its relative dominance value is greater than a new random number, it wins ($w_i = 1$), else it loses ($w_i = 0$):

$$w_i = \begin{cases} 1 & \dfrac{DOM_i}{DOM_i + DOM_j} > RND(0,1) \\ 0 & else \end{cases} \qquad (1)$$

The stochastic effect is introduced to allow for dominance reversals. To reflect the self-reinforcing effects of victory and defeat (Hsu & Wolf 1999; Hemelrijk et al. 2008a), dominance values are updated by increasing the dominance value of the winner and decreasing that of the loser by the same amount:

$$\begin{aligned} DOM_i &= DOM_i + \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) * STEPDOM \\ DOM_j &= DOM_j - \left(w_i - \frac{DOM_j}{DOM_i + DOM_j} \right) * STEPDOM \end{aligned} \qquad (2)$$

This positive feedback is 'dampened' because a victory of a higher ranking opponent increases its relative *Dom*-value only slightly, whereas an (unexpected) success of the lower ranking individual increases its relative dominance value by a greater change. To keep *Dom*-values positive, their minimum value is, arbitrarily, set at 0.01.

The change in *Dom*-values is multiplied by a scaling factor, called *StepDom*, which varies between 0 and 1 and represents the intensity of aggression (Hemelrijk 1998; Hemelrijk 1999a) (see Parameters and Experimental setup). High values imply a great change in *Dom*-value after a fight, and thus indicate that single interactions (e.g. involving biting) may strongly influence the future outcome of

conflicts. Conversely, low *StepDom*-values represent low impact (e.g. threats or slaps).

Winning an interaction includes chasing the opponent over a distance of one unit and then turning randomly 45 degrees to right or left in order to reduce the chance of repeated interactions between the same opponents. The loser responds by fleeing under a small random angle over a predefined *FleeingDistance*.

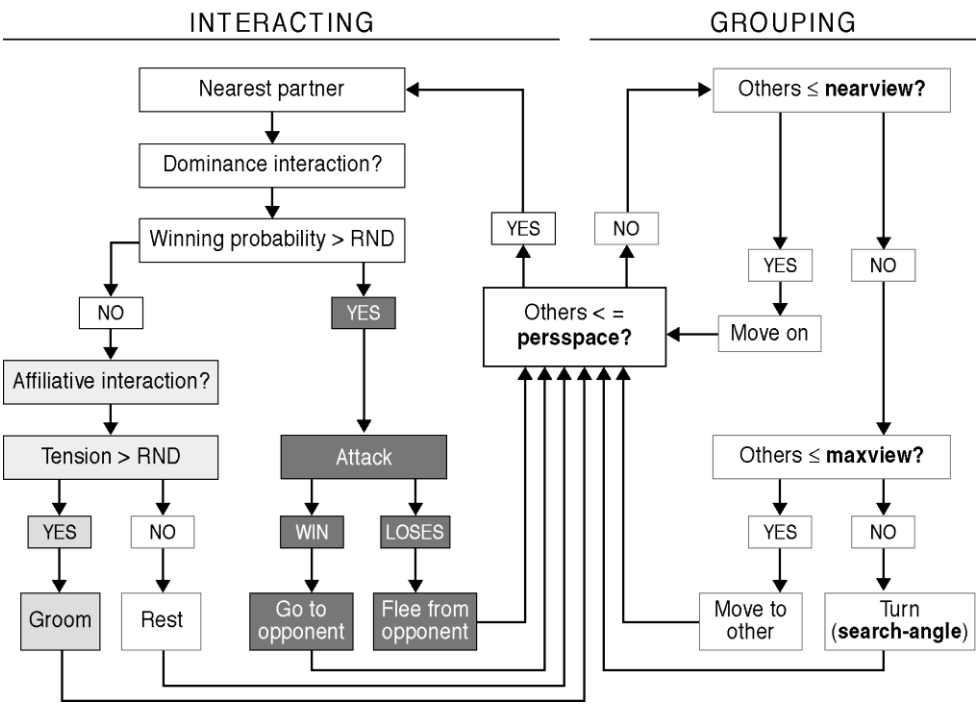

Figure 1. Rules of behavioural interaction. In light grey boxes the new rules of GrooFiWorld related to grooming are indicated. In white boxes the grouping rules, and in black boxes the rules for dominance interactions from DomWorld (Hemelrijk 1999a; Hemelrijk 2000a).

Grooming rules

If an individual meets another in its *PersSpace* and when it has decided on the basis of a 'mental' battle that it is too dangerous to attack, the individual considers whether or not to groom its partner (Figure 1). Grooming behaviour is induced by the level of *Anxiety*, which ranges from very relaxed to very tense, represented by a scale from 0 to 1. If the *Anxiety* value is lower than a random number, the individual will display 'non-aggressive' proximity; otherwise, if *Anxiety* is higher, it will groom its partner (Figure 1). After grooming both partners turn over a small angle (45°) randomly to the right or left in order to avoid repeated interactions with the same partner. Grooming reduces *Anxiety.* In line with empirical evidence (Meller et al. 1980; Fabre-Nys et al. 1982; Keverne et al. 1989; Aureli & van Schaik 1991; Schino & Troisi 1992; Martel et al. 1995; Castles & Whiten 1998; Das et al. 1998; Graves et al. 2002; Shutt et al. 2007), it does so more strongly in the groomee (with *AnxDcrGree*) than in the groomer (with *AnxDcrGrmr*) (Table 3). During periods without grooming *Anxiety* increases, which is consistent with opiate-dependent motivation to groom in real primates (Fabre-Nys et al. 1982; Keverne et al. 1989). This increase is updated after every activation with *AnxInc.* Furthermore, inspired by the observed increase in scratching after a fight in real primates (Aureli et al. 2002), in the model, after a fight *Anxiety* increases with *AnxIncFght* for both opponents.

Parameters and Experimental Set-up

Many parameters that have been used in earlier studies were kept at the same value, namely the *NearView, MaxView, FleeingDist, SearchAngle* and *StepDom* values. Note that *StepDom* values (that reflect intensity of aggression) differ between the sexes (on the basis of the stronger muscular structure of males than females) and between dominance styles reflecting the tendency of individuals in despotic societies to bite relatively more (and slap and threaten less) than in egalitarian ones (Hemelrijk 1998; Hemelrijk 1999a; Hemelrijk 2000c; Hemelrijk et al. 2003; Hemelrijk & Wantia 2005) (Table 3). We used 12 individuals to represent the number of adults in a group of primates. Since in empirical studies the percentage

of females is lower in egalitarian macaques with approximately 70% females than despotic macaques with approximately 80% females, we have set the sex ratio at low and high aggression intensity accordingly (with 8 females, 4 males at low intensity and 10 females and 2 males at high intensity) (Caldecott 1986; Ménard 2004; Wantia 2007). The initial dominance values we set at 16 for females and 32 for males, reflecting the initially higher winning chance of males due to sexual dimorphism in fighting power resulting from differences in body weight, physiology and weaponry.

In order to tune the frequency of grooming to 20% of the time as indicated for despotic societies of real primates by Dunbar (1991), we had to increase *PerSpace* from 4 to 8 units (reflecting a tendency to interact with others over larger distances), to increase the risk-sensitivity of individuals by increasing the number of mental battles 'ego' had to win before starting a real dominance interaction (in order to reduce the frequency of aggression) (*RiskSens*, Table 3) and to tune the *Anxiety*-related parameters (see Table 3).

To understand what caused the patterns of affiliation in the model, each of four assumptions related to grooming and fighting were switched off in turn. The simulation was run in turn 1) without the self-reinforcing effects of winning and losing fights, 2) without the grooming inducing effect of anxiety, 3) without the dependence of grooming on the risks to attack and 4) without the selection of interaction partners on the basis of spatial proximity.

First, when switching off the self-reinforcing effects of winning and losing, we gave the individuals *Dom* values that were constant. We took these values from runs with the corresponding intensity of aggression, because hierarchical differentiation was greater at a high than at a low *StepDom*. We took the values from the middle (i.e. period 230) of the interval between periods 200 and 260, because in this interval the *Dom* values were considered to have stabilised (Hemelrijk & Gygax 2004), since the average *Dom* values between period 200 and 230 are significantly correlated with those between 230 and 260 (Kendall Tau,

N=10, High intensity Tau = 0.88 ***, Low intensity Tau=0.85** two tailed probability).

Second, to switch off the grooming inducing effect of *Anxiety* implies that we made grooming independent of the value of *Anxiety*. In this case, the individual always groomed its partner whenever it refrained from attack because of high risks.

Third, switching off fear-based grooming, implied that we made grooming independent of the risks of defeat, i.e. upon meeting another individual in its *PerSpace* we gave the individual a 50% chance to either consider grooming it or attacking it. After choosing between attacking and grooming, the risk-sensitive decision procedure was used to decide whether the individual actually attacked and the anxiety-based rule was used to decide whether it actually groomed. If the individual decided to refrain from interacting, it rested at its location.

Fourth, to switch off proximity-based interactions, interaction partners were chosen at random independent of their proximity in space.

Data collection and Analysis

Every run consisted of 260 periods and each period consisted of 240 activations (the number of individuals (i.e. 12) times 20). Data were collected from period 200 to 260 to exclude any bias caused by transient values. Data consisted of every change in spatial position and in heading direction of each individual and, as regards social interactions, we recorded (1) the identity of the attacker and its opponent, (2) that of the winner/loser, (3) the updated *Dom* values of the individuals, (4) the identity of the groomer and groomee and (5) the updated *Anxiety* value of the individuals. For each model (the complete model and the four controls with a missing assumption) 10 independent simulations were run for each of the two aggression intensities (high and low). The results are shown here per condition as the average statistic of these 10 runs with their combined probability using the improved Bonferroni procedure (Hochberg 1988). Patterns apparent in empirical studies of egalitarian and despotic macaques (Table 1) were tested for by means of (combined) one-tailed probabilities (Tables 4 and 5), all the other

patterns were tested with two-tailed probabilities (Tables 6 and 7). To test for differences in patterns between high and low intensity of aggression, we used the Mann Whitney U test whereby we compared the statistics between 10 runs at a high and 10 runs at a low intensity of aggression (see Tables 4, 5, 6).

The percentage of time females spend in fighting (or in grooming) is calculated as the number of fights (grooming) in the group divided between the total number of activations. The percentage of interaction time spend in grooming is the frequency of grooming divided by that of grooming plus that of fighting.

The hierarchical differentiation among all females was measured by the coefficient of variation of *Dom* values (standard deviation divided by the mean). For each run the average value was calculated (over period 200-260) and this was averaged over 10 runs. Higher values indicate greater rank distances among individuals (Hemelrijk 1999a). Hierarchical differentiation is also reflected in the empirical behavioural measure of the degree of unidirectionality of aggression (Hemelrijk 1990a; Thierry 2004), which we show also (Table 4).

The diversity of partners with whom a female interacts is measured by the Berger-Parker dominance index (Southwood 1978) by dividing an individual's frequency of grooming with its most favourite partner by its total grooming frequency.

The rank of group members we calculated as the average *Dom* value of each individual per run over periods 200 - 260. We used an average measure, because we correlated it with an average measure of aggressive and affiliative acts, i.e. data were summed over the whole interval of period 200-260. Apart from the average dominance value as a measure of rank we applied also a behavioural measure used in empirical studies, namely the average percentage of winning (Hemelrijk et al. 2005).

The degree to which dominant individuals (both males and females) occupy the centre was measured by a correlation between an individual's average *Dom* value and the average spatial direction of others around it. The centrality of each individual is calculated by means of circular statistics by drawing a unit circle

around ego and projecting the direction of other group members as points on the circumference of this circle (Mardia 1972). The connection of these points with ego's location results in vectors. The length of the mean vector represents the degree to which group members relative to ego form a cluster. Thus, longer mean vectors indicate a more peripheral, and hence, less central location of ego. Therefore, centrality of dominants is represented by a negative correlation between rank and the length of average vector (indicating the average direction of others).

In empirical studies reconciliation has been measured often by the PC-MC method (i.e. Post-Conflict versus Matched-Control). Here, we have used its improved version (de Waal & Yoshihara 1983; Veenema et al. 1994). In it a comparison is made between the moment in which grooming occurs during a short interval after a conflict, the so-called Post-Conflict period, and the moment it occurs in a control period of the same length (ten minutes), the Matched-Control period, taken a day later at the same time. Because our model is event-driven, we use its average number of fights over the interval 200-260 (of 2196 acts at high intensity) and the average frequency of fights per hour of rhesus monkeys of 0.2 per hour per individual (de Waal 1977) and a day length of about 13h to estimate that the interval of ten minutes is approximated by three activations in the model (one activation is about 3.8 min) and the interval of one day is approximately represented by one period. These are of course abstractions but results appear to be robust (see Sensitivity to parameter changes). Dyads were classified as 'attracted', when grooming happened earlier in the Post-Conflict period than in the Matched-Control. Pairs were classified as 'dispersed', when grooming happened in the reverse way, and as 'neutral', when grooming happened exactly at the same time or did not happen at all. Following (Veenema et al. 1994), we calculated the conciliatory tendency, CT, of the group as:

$$CT = \frac{NumberAttractedPairs - NumberDispersedPairs}{TotalNumberOfConflictPairs}$$

To measure the conciliatory tendency of each female with each of its group members, we calculated per pair the number of times they groomed sooner after a fight than in the matched control (attracted events) minus the cases where the opposite happened (dispersed events) divided by the total number of fights of the pair.

Correlations between the distribution of grooming, proximity, aggression and reconciliation among females, and between social interactions and rank were measured by means of the Tau-Kr correlation as described by Hemelrijk (Hemelrijk 1990a; Hemelrijk 1990b), which is frequently used in studies of animal behaviour (Gilby & Wrangham 2008; Lu et al. 2008; Ward et al. 2008). The advantage of this statistic is that it is animal-centred, because it takes variation in grooming and aggression between individuals into account by measuring the correlation between the corresponding rows of two social interaction matrices and because it accounts for the dependence of data in an interaction matrix. The level of significance was calculated using 2000 permutations (Hemelrijk 1990a; Hemelrijk 1990b). We tested for unidirectionality of attack and reciprocity of grooming by correlating an actor and receiver matrix with the Tau-Kr correlation. Note that unidirectionality and reciprocity are opposite correlations: a significantly negative correlation implies unidirectionality, whereas a significantly positive correlation implies reciprocity (Hemelrijk 1990a).

Whether grooming was directed up the hierarchy and to partners of similar rank was computed by the Tau-Kr correlation between, on the one hand, the grooming matrix and, on the other hand, respectively, the partner-rank-matrix (with the average *Dom* values of grooming partners in the rows) and the similar-rank-matrix (filled with zeros apart from the partners closest and second closest in rank, which are indicated as 1's). Note that the higher-ranking individuals have higher *Dom* values. Thus, a significantly positive correlation with the partner-rank-matrix corresponds to grooming being directed up the hierarchy, and a significantly positive correlation with the similar-rank-matrix corresponds to a high degree of grooming among individuals of similar rank.

To test the valuable-relationship hypothesis, we defined valuable relationships on the basis of the grooming frequency as is done by primatologists (e.g. Arnold & Barton 2001; Cooper et al. 2005; Majolo et al. 2005). We used the frequency of grooming that occurred per dyad outside of the context of reconciliation in order for correlations with reconciliation not to be circular. We determined the degree of reconciliation with valuable partners by means of the Tau-Kr correlation between the matrices of the conciliatory tendency per dyad and that of the frequency of grooming per dyad outside the context of fighting (by subtracting the acts of conciliatory grooming from the matrix with all grooming acts). A significant positive correlation reflects that reconciliation is more frequent with partners that are more valuable.

Results

Empirical patterns

As regards our distinction of macaques in egalitarian and despotic, we updated the classification of Thierry (1990; 2000) with new data on Tibetan macaques (*Macaca thibetana*) (Berman et al. 2004) and Assamese macaques (*Macaca assamensis*) (Cooper & Bernstein 2008). Therefore, we rated as egalitarian Barbary macaques (*Macaca sylvanus*), bonnet macaques (*Macaca radiata*), stumptailed macaques (*Macaca arctoides*), lion-tailed macaque (*Macaca silenus*), Celebes crested macaque (*Macaca nigra*) and tonkean macaques (*Macaca tonkeana*) and as despotic we classified long-tailed macaques (*Macaca fascicularis*), Japanese macaques (*Macaca fuscata*), rhesus macaques (*Macaca mulatta*), pigtailed macaques (*M. nemestrina*), Tibetan macaques and Assamese macaques. Regarding the dominance style (Table 1), the frequency of unidirectional aggression, which is a measurement related to the hierarchical gradient in macaques, appears to be higher in despotic than in egalitarian species (Thierry 2004); further, frequency of aggression is lower (Thierry 1990) and average distance among all females is greater (de Waal & Luttrell 1989; Thierry 1990). Besides, for the despotic Japanese macaques, it has been reported that dominants are in the center of the group (Itani 1954; Imanishi 1960; Yamada 1966). As to affiliative patterns, reconciliation occurs

in both types of species, and is more frequent in egalitarian species (Thierry 2004). Grooming is reciprocated in both egalitarian and despotic species. Further, grooming is directed up the hierarchy and to others of similar rank only in despotic species. Reconciliation is directed significantly more often to partners that are more valuable in several despotic species and according to a single study also in an egalitarian species, *Macaca arctoides* (Call et al. 1999).

Tuning the model

As described in the methods, we first tuned the percentage of time spent on grooming at a high intensity of aggression so that it resembled that of empirical data for despotic macaques (Dunbar 1991). Subsequently, we, unexpectedly, observed reconciliation. Since there are more precise data on the conciliatory tendency of despotic macaques than on their percentage of time spent on grooming, we subsequently tuned the conciliatory tendency to that of despotic macaques by adjusting the risk sensitivity further (7 in Table 4).

Emergent patterns of dominance style and affiliation in the model

As to the two dominance styles in our model, we first confirmed that they still emerged, like they did in the earlier DomWorld model without grooming (Hemelrijk 1999a; Hemelrijk 2000a). In GrooFiWorld, at a high intensity of aggression, the hierarchy appeared to be significantly steeper than at a low intensity, aggression was more unidirectional, time spent on fighting was less, average distance among all females was greater and the spatial structure with dominants in the centre and subordinates at the periphery was more conspicuous (1-5 in Table 4; 1, 5-7 in Table 2C).

We confirm the resemblance of the affiliative patterns in the model to empirical data (Tables 1, 4): The conciliatory tendency appeared to be significantly higher at a low aggression intensity than at a high one (7 in Table 4); grooming appeared to be reciprocated at both intensities (8 in Table 4); a number of significant correlations were confined to a high aggression intensity, namely individuals direct their grooming significantly 1) up the hierarchy, 2) to others of

similar rank, and 3) they reconcile more often with more valuable (grooming) partners (9-11 in Table 4). The only difference to empirical data concerns the absence in the model of more frequent reconciliation with valuable partners at low aggression intensity (11 in Table 4). However, in empirical data this correlation for the valuable relationship hypothesis was found only in a single empirical study of an egalitarian species (Call et al. 1999) and it was based on a different method, i.e. the time rule method, whereas in the model we use the MC-PC method.

Causation of patterns in the model and model-based hypotheses

In order to understand what caused these patterns of affiliation in the model, we took out four different assumptions in turn (see Parameters and Experimental Set-up). This reduced the number of emergent patterns. Switching off the self-reinforcing effect of the outcome of a fight did not affect the patterns qualitatively, but switching off the grooming-inducing effect of *Anxiety* changed three patterns of the 28 (11%) (indicated in bold in Table 5). Making grooming independent of fear of defeat changed seven patterns (29%) and choosing partners at random independent of spatial proximity changed 20 patterns (75%). Thus patterns arose mainly from the social-spatial group structure and secondly from grooming being dependent on fear of defeat.

To explain the emergence of each of the affiliative patterns in the model (Table 4), we proceed now by studying the effects of each of the four above-mentioned assumptions by taking them out (Table 5). This process leads to a number of model-based hypotheses for empirical data (Table 2).

The emergence of grooming up the hierarchy depended on grooming being based on fear of being defeated (without this assumption the pattern disappeared) and on the intensity of aggression (since it is absent at a low intensity of attack). This arises because the hierarchical differentiation is stronger at a high aggression intensity compared to a low one, and aggression is more unidirectional (1, 2 in Tables 4 and 5). Thus, when grooming depends on fear of defeat and the difference in rank between the partners is high, lower ranking ones will usually groom higher ranking ones and rarely attack them (as a consequence of Eq 1).

	Real macaque societies		Model	
Intensity of aggression	**Despotic**	**Egalitarian**	**High**	**Low**
Dominance Style				
1) Gradient of Hierarchy	NA	NA	0.86	0.11
Gradient of the hierarchy High > Low	NA		U=100 ***	
2) Unidirectionality of aggression	True	NS	-0.45**	0.18*
Unidirectionality of aggression High > Low	True		U=99 ***	
3) Time spent fighting (%)			15-16%	16-18%
Fighting % High < Low	NA		U=97 ***	
4) Mean distance among group members	Low	High	17	10
Average distance High < Low	NA		U=100 ***	
5) Centrality of Dominants (Tau)	True	NA	-0.56*	0.06
Centrality High > Low	NA		U=100 ***	
Affiliative patterns				
6) Time spent grooming (%)	8-15%	NA	***13-23 %***	28-30 %
7) Conciliatory tendency	7-18%[1]	20-50%[2]	***7-17 %***	16-22 %
Conciliatory tendency High < Low	True[1]		U=98 ***	
TauKr Correlations				
8) Grooming Reciprocation	True	True	0.31**	0.45**
9) Grooming up the hierarchy	True	NS	0.44**	0.05
10) Grooming partners of similar rank	True	NS	0.25**	0.04
11) Reconciliation with valuable partners	True	True	0.21**	**-0.04**

Table 4. Dominance style and affiliative patterns (for measurements see methods). One tailed p-values of tests are combined via the improved Bonferroni method (n= 10): * p<0.05, **p<0.01, ***p<0.001. In bold italics are the two percentages which quantities were tuned to empirical data (although reconciliation in itself was emergent). In bold are results that differ from empirical data. [1, 2] Data of conciliatory tendencies of *Macaca nemestrina*[1] and *Macaca silenus*[2] were excluded, because these were considered as outliers.

Grooming reciprocation (8 in Table 4, 5) arose from spatial structure, because it was disrupted only by taking out the socio-spatial structure, but not by taking out any of the other three assumptions. This means that, because certain individuals are often in close proximity, they will groom each other mutually, resulting in reciprocation. Furthermore, reciprocation appeared to be strongest in the experimental control condition where grooming did not depend on fear of defeat, and next strongest at a low aggression intensity. This arose because reciprocation was weakened less by differences in dominance, because these are smaller at low intensity of aggression (1, 2 in Table 4 and 5).

Besides, at high aggression intensity, but not at a low one, individuals automatically more often groomed partners that were similar in rank. This was due to grooming being based on fear of defeat, and due to spatial structure (10 in Tables 4 and 5). At a high intensity of aggression, not only a steep hierarchy develops, but also a spatial structure with dominants in the centre and subordinates at the periphery that is clearer than at a low intensity (1, 5 in Table 4; 1, 7 in Table 2C). Therefore individuals of similar rank are closer together. Thus, at high aggression intensity because individuals will groom up the hierarchy, while meeting mostly others of similar rank, this means that everyone grooms those of similar rank more often than those of lower rank, and, those of similar rank approximately as often as those of higher rank. Therefore, a correlation for grooming among individuals of similar rank results. At a low intensity of aggression, spatial centrality of dominants is absent (5 in Table 4) and due to the small rank differences grooming is directed neither up the hierarchy, nor to others of similar rank (9, 10 in Table 4).

The occurrence of reconciliation in our model is a side-effect of spatial proximity, since it is almost absent if interaction partners are chosen at random (7 in Table 5). Thus, reconciliation in the model is largely due to the higher probability of two opponents to be close to each other immediately after a fight (i.e. Post-Conflict) than otherwise (during the Matched-Control).

Furthermore, the conciliatory tendency is reduced at high intensity of aggression as a side-effect of the spatial structure and the dependence of grooming on the fear of defeat; without these assumptions the conciliatory tendency is independent of intensity of attack (7 in Table 5). This happens for three reasons (to be tested in empirical data, Table 2): at a high aggression intensity the spatial structure is more static (10 in Table 2C), average inter-individual distance is larger (6 in Table 2C), and centrality of dominants is greater (7 in Table 2C). First, spatial structure is more static at high aggression intensity, which is apparent from the stronger spatial assortment by rank of individuals (5 in Table 4), from the lower diversity of partners at high intensity of aggression than at a low one (16 in Table 6, 10 in Table 2C), and from the fact that the correlation between proximity and conciliatory tendency is significantly stronger at a high aggression intensity than at a low one (22 in Table 6; 11 in Table 2C). Therefore, former opponents may have been more often close to each other not only immediately after the conflict (in the post conflict period) but also in the matched control. Consequently, it is more likely that they groom each other in the matched control. If this happened at an earlier moment than after the conflict (in the post conflict period) it reduced the conciliator tendency. Second, due to the greater differences in rank, individuals are further apart (1, 4 in Tables 4 and 5) and groom less often both as calculated as the percentage of time and the percentage of interactions at a high than at a low intensity of aggression (13, 14 in Table 6; 8, 9 in Table 2C). Thus, they will automatically also groom less often immediately after a conflict, thus reconcile less than at a low aggression intensity (7 in Tables 4, 5). Third, at a high intensity of aggression grooming and conciliatory tendency are reduced because of the combination of spatial structure and the fear of defeat: If the fear of defeat is removed, the conciliatory tendency at a high intensity of aggression is higher than in the complete model (4 in Table 7), because spatial assortment according to dominance (i.e. spatial centrality of dominants) is weaker than in the complete model (3 in Table 7). Thus, dominants are relatively less often activated (to fight) and this increases the relative frequency of grooming because subordinates are aggressive less often (2 in Table 6). Thus without fear of defeat the percentage of

time spent and interaction time spent on grooming is higher (13,14 in Table 6), so that it is higher than it is at a high intensity of aggression in the complete model (1, 2 in Table 7) and thus the percentage of time spent on reconciliation is higher also (5, 6 in Table 2A). Similarly, in the complete model, because at a lower intensity of aggression spatial structure is weaker than at a high intensity also, the percentage of grooming of the total number of interactions (aggressive plus grooming) is higher at a low than high intensity of aggression (14 in Table 6). Thus the conciliatory tendency is lower at a high than low intensity also (5, 6 in Table 2A).

Further, at a high intensity of attack reconciliation was directed mostly to those partners that are more valuable (in terms of grooming outside the context of reconciliation, 11 in Table 4) and this was stronger than at low intensity (23 in Table 6). This is due to (1) stronger effects of spatial proximity (2) high intensity of attack, and (3) fear of defeat, because without these traits there is no reconciliation with valuable partners (11 in Table 5) or it is significantly weakened (23 in Table 6). As regards spatial proximity, the stronger correlation for valuable relationships arises because the spatial structure at a high intensity is more rigid and therefore both reconciliation and grooming are correlated stronger with the proximity between partners than at a low intensity (20 and 22 in Table 6; 11 in Table 2C); thus, the two patterns of grooming and reconciliation are correlated too at a high, but not at a low intensity (11 in Table 4). As to the second and third cause, at a high intensity of aggression (due to the strong hierarchical differentiation) conciliatory tendency like grooming behaviour appears to be directed up the hierarchy (9 in Table 6; 1 in Table 2B), although this holds only when grooming is done out of fear of defeat (9 in Table 6) like in 'normal' grooming which does not occur after a conflict (9 in Table 4, 5).

Other patterns in the model and model-based hypotheses

There are other patterns in the model that are of interest in it self and for study in empirical data (Table 2). For instance, in the model higher ranking individuals appear more aggressive due to the lower risk involved (2 in Table 6),

	No self-reinforcing effects		No anxiety induced grooming		No fear of defeat		No spatial structure	
Intensity of aggression	High	Low	High	Low	High	Low	High	Low
Dominance Style								
1) Gradient of the hierarchy	0.73	0.08	0.74	0.09	0.62	0.07	0.75	0.10
Gradient of the hierarchy High > Low	U=100 ***		U=100 ***		U=100 ***		U=100 ***	
2) Unidirectionality of aggression	-0.41**	0.16**	-0.39**	0.20**	-0.17*	0.25**	-0.68**	**-0.15***
Unidirectionality of aggression High > Low	U=100 ***		U=100 ***		U=97 ***		U=100 ***	
3) Time spent fighting (%)	14-15%	17-18%	12-15%	13-14%	**7-9%**	**6-7%**	**31-37%**	**26-27%**
Fighting % High < Low	U=100 ***		**U=50.5 NS**		**U=96 NS**		**U=100 NS**	
4) Average distance among group-members	17.07	10.13	16.83	11.68	18.65	15.51	**NA**	**NA**
Average distance High < Low	U=100 ***		U=97 ***		U=96 ***		**NA**	
5) Centrality of dominants	-0.52**	-0.10	-0.49*	-0.27	-0.41*	0.04	**NA**	**NA**
Centrality High > Low	U=90 **		U=76 *		U=90 **		**NA**	
Affiliative Patterns								
6) Time spent grooming (%)	16-18 %	27-30 %	16-32%	**34-38%**	19-24 %	22-27 %	**41-42 %**	**41 %**
7) Conciliatory tendency	10-14 %	14-21 %	5-20 %	19-25 %	**19-28 %**	20-28 %	**0-2 %**	**0-5 %**
Conciliatory tendency High < Low	U=100 ***		U=99 ***		**U=56 NS**		**U=68 NS**	
Tau-Kr Correlations								
8) Grooming reciprocation	0.39**	0.50**	0.33**	0.47**	0.69***	0.67***	**-0.52**	**0.00**
9) Grooming up the hierarchy	0.46**	0.06	0.39**	**0.11***	**0.01**	0.02	0.59**	0.07
10) Grooming those of similar rank	0.18*	0.06	0.18**	-0.01	**0.06**	0.04	**0.08**	-0.05
11) Reconciliation with valuable partners	0.23*	-0.03	0.17*	-0.03	0.04*	0.04	**NA**	**NA**

Table 5. Dominance style and affiliative patterns when taking out different assumptions (see methods). One tailed p-values of tests are combined via the improved Bonferroni method: * p<0.05, **p<0.01, ***p<0.001. Results that differ from the complete model (in Table 4) are shown in **bold**.

	Model		No self-reinforcing effects		No anxiety induced grooming		No fear of defeat		No spatial structure	
Intensity of aggression	High	Low	High	Low	High	Low	High	Low	High	Low
1) Berger-Parker dominance index for grooming partners	0.24	0.20	0.22	0.20	0.21	0.20	0.22	0.23	0.19	0.18
Correlations between rank and[1]										
2) Aggression given	0.84**	0.61*	0.82**	0.56	0.83**	0.53*	0.74**	0.33	0.89***	0.58*
3) Aggression received	-0.86***	-0.52*	-0.90***	-0.54	-0.89**	-0.38	-0.86***	-0.40	-0.90***	-0.61*
4) Number of fights lost	-0.86**	-0.51	-0.84**	-0.39	-0.85**	-0.44	-0.78**	-0.45	-0.87***	-0.57**
5) Anxiety	-0.59**	-0.17	-0.61*	-0.09	-0.43	-0.25	-0.25*	0.00	-0.54*	0.18
6) Grooming given	0.02	-0.14	0.20	-0.09	-0.21	0.00	0.52*	0.04	-0.85**	-0.48*
Correlations between[2]										
7) Conciliatory tendency and proximity of the partner	-0.16	0.04	-0.19	-0.01	-0.12	0.05	0.02	-0.07*	NA	NA
8) Grooming and proximity of the partner	-0.55**	-0.42**	-0.56**	-0.42**	-0.50**	-0.40**	-0.42**	-0.46**	NA	NA
9) Conciliatory tendency and rank of the partner	0.21**	-0.01	0.25*	0.01	0.10	-0.05	-0.14	-0.04	NA	NA
Difference between aggression intensities for[3]										
10) Aggression given	U=88 **		U=92 **		U=91 **		U=90 **		U=88 **	
11) Aggression received	U=89 **		U=98 ***		U=100 ***		U=100 ***		U=96 ***	
12) Number of fights lost	U=98 ***		U=99 ***		U=97 ***		U=90 **		U=86 **	
13) Grooming-time percentage	U=100 ***		U=100 ***		U=100 ***		U=88 **		**U=56 NS**	
14) Grooming-interaction percentage	U=100***		U=100***		U=100***		U=99**		U=100***	
15) Grooming reciprocation (Tau-Kr)	U=68 NS		**U=78** *		**U=81** *		U=66NS		**U=100** ***	
16) Berger-Parker dominance index	U=87**		U=100 ***		U=61NS		U=58NS		U=74NS	
17) Rank and anxiety (tau)	U=96 ***		U=91 **		U=68 NS		U=110 NS		U=67 ***	
18) Grooming up the hierarchy	U=100***		U=100 ***		U=100 ***		U=55 NS		U=100 ***	
19) Grooming those of similar rank	U=95 ***		U=70 NS		U=85 **		U=51 NS		U=84 **	
20) Grooming and proximity of the partner (Tau-Kr)	U=77 *		U=90 **		U=80 *		U=66 NS		NA	
21) Conciliatory tendency up the hierarchy (Tau-Kr)	U=91 **		U=99 ***		U=86 **		U=92 ***		NA	
22) Conciliatory tendency and proximity of the partner (Tau-Kr)	U=91 **		U=97 ***		U=89 **		U=68 NS		NA	
23) Conciliatory tendency with valuable partners (Tau-Kr)	U= 90 **		U=97 ***		U=84 **		U=51 NS		NA	

Table 6. Different variables correlated to the ranks of individuals for the model when taking out different assumptions (see methods). [1]: Kendall rank correlations. [2]. Tau-Kr correlations. [3]: Mann Whitney- U test. Two tailed p-values combined with the improved Bonferroni method: * p<0.05, **p<0.01, ***p<0.001.

and less anxious (but only at high intensity of aggression) (5 in Table 6; 12 in Table 2C) because they have lost fewer fights (4 in Table 6) and these effects are stronger at a high than low aggression intensity (10-12 in Table 6; 4 in Table 2C).

Further, both at a high and a low intensity of aggression, there is no correlation between grooming and rank (6 in Table 6; 2 in Table 2A). This is remarkable at high intensity of aggression, because lower ranking individuals are more anxious and therefore, they may be expected to groom others more often. The absence of this correlation arises from the fact that a high grooming frequency by low ranking individuals is counteracted by the spatial social structure (5 in Table 5); due to their peripheral positions, low ranking individuals have fewer opportunities to interact with others than dominants do and therefore, despite their greater tendency to groom, they do not groom more often than dominants.

	Complete Model	**No fear of defeat**	**Mann Whitney U test**
1) Percentage of time spent grooming	13-23 %	19-24 %	U=92 **
2) Percentage of interaction time spent grooming	45-59%	72-77%	U=100 ***
3) Centrality	-0.56*	-0.41*	U=76 *
4) Conciliatory tendency	7-17 %	19-28 %	U=100 ***
5) Reconciliation with valuable partners	0.21**	0.04*	U=92 ***

Table 7. Comparison between different variables of the complete model and the model without fear of defeat at high intensity of aggression (Mann Whitney U test, two-tailed).

Sensitivity of patterns to parameter changes and the measure of rank

As regards the sensitivity to changes of parameter, the affiliative patterns were insensitive to different values of parameters related to *Anxiety*. Values ranging from 0.001% to 10% for *AnxInc* and values from 0.05 to 0.15 for *AnxIncFight, AnxDcrGree* and *AnxDcrGrmr* (whereby *AnxDcrGree* was kept at higher values than *AnxDcrGrmr*) changed the level of anxiety, but did not change results qualitatively.

To obtain a sufficiently high number of interactions (both of grooming and fighting) to detect affiliative patterns statistically, a *Perspace* 8 was necessary, whereas a value of 4 was too low. Furthermore, two mental fights (Equation 1) before initiating a dominance interaction (*RiskSens* = 2) were needed in order to make the frequency of grooming higher than that of fighting like in empirical data. Besides, in empirical data the percentage of time spend fighting was lower in fierce than mildly aggressive species. This was true when comparing the percentage of fighting at high versus low intensity of aggression in the model for *RiskSens* 1 and 2, but not for higher values of *RiskSens*.

Results of reconciliation were similar if we prolonged the period of Matched control from three activations to five and to ten activations.

Since in the empirical data average dominance cannot be accessed directly like in our model, we also tested all correlations with a measure of dominance, i.e. their average percentage of winning, which can be measured in real behaviour (Hemelrijk et al. 2005). All results of Table 4 and 6 remain similar (also in the strength of the significance), apart from two correlations in Table 6: when correlating with the average percentage of winning as a measure of dominance, at a high intensity of aggression, higher ranking individuals groom others significantly less and at a low intensity of aggression, the negative correlation between aggression received and dominance is no longer significant (data available on request). It should be noted however, that to explain patterns of our simulation, the correlations with average dominance value are of greater interest than with percentage of fight won because the average dominance value is a more direct cause of behaviour in the model.

Discussion

Our model presents us with an integrative theory of affiliative behaviour in primates, because it gives a coherent explanation for aspects of many of the patterns of affiliation typical of egalitarian and despotic macaques. It does so, while it only makes the 'cognitive' assumptions that individuals are 1) intending to group,

2) they recognise each others rank (here it is unspecified whether this is due to the other's body posture, former experiences with the other or due to observations of interactions among other group members, or some or all of these), 3) in their initiation of aggression they are sensitive to risks of losing a fight, 4) their grooming is induced by the expectation of losing a fight, and 5) the wish to decrease their anxiety. Anxiety is induced by fighting and increases with the duration of not being groomed. Thus, remarkably, in contrast to views of others (Seyfarth 1977; de Waal & van Roosmalen 1979; de Waal & Luttrell 1988; Arnold & Aureli 2006), our model ignores a number of the specific cognitive assumptions that have been made for primates. In it individuals only need minimal information. Thus, our model generates a) reciprocation without that the individual keeps records in its memory of services given to and received from each of its partners, b) grooming up the hierarchy without an intention to receive support in exchange, c) grooming others of similar rank without competition for higher-ranking grooming partners or attraction to higher ranking-partners, d) reconciliation without a conciliatory predisposition or a memory of, and a selective attraction to, a former opponent and e) reconciliation with partners that are more valuable without any estimate of the quality of the relationship. Besides, it reproduces the differences between egalitarian and despotic species in their conciliatory tendency without a difference between low and high intensity of aggression in possibilities to negotiate (Silk 1997) and without reconciliation reducing conflict escalation (de Waal 1986). Our model also provides us with coherent mechanisms for the systematic variation hypothesis or the co-variation hypothesis (Thierry 1985; Thierry 1990; Castles et al. 1996; Thierry 2000; Cooper & Bernstein 2002; Thierry 2004; Thierry 2007; Thierry et al. 2008).

As to the function of reconciliation, our model does not represent this specifically in its rules, since reconciliation emerges from a rule that makes individuals groom merely to reduce anxiety. Thus, its function is to reduce anxiety. However, in our model (like in reality) grooming occurs more often after a fight than at other times. Therefore, if similar processes in reality cause patterns of

reconciliation, such emergent patterns of reconciliation after a fight may still function to repair a relationship.

Causation of patterns in the model

The causation of each of the affiliative patterns in the model is as follows. First, grooming up the hierarchy results when aggression intensity is high and the hierarchy is steep because individuals seldom dare to attack higher ranking ones, and therefore in order to reduce their anxiety they groom up the hierarchy instead. When aggression intensity is low, the hierarchy is weak, thus individuals experience a smaller risk to attack higher ranking ones and therefore there is no such pattern.

Other patterns depend on the spatial configuration. Because interactions take place in space, individuals are more likely to be close to those they have recently interacted with than to others. Therefore, they are more likely to groom one another after an interaction than at other times. Thus, we observe patterns of both reconciliation of fights and reciprocation of grooming. In the model, aggression determines the spatial structure of the group (Hemelrijk 2000a). At a high intensity of aggression a spatial structure develops through the continuous fleeing of low ranking individuals. Therefore, subordinates end up at the periphery and dominants are located in the centre, and thus individuals are closer to others of similar rank. Such a rank-assortment is virtually absent at a low intensity of aggression (Hemelrijk 1999a). Therefore at a high intensity of aggression, since individuals are closer to others of similar rank, they usually groom others of similar rank. Furthermore, at a high intensity of aggression dominants interact more often than subordinates, because dominants are surrounded at all sides by others due to their spatial centrality. Consequently, because dominants are more often aggressive than subordinates are, the percentage of interaction time spent in grooming is lower at a high than at a low intensity of aggression. Because individuals groom relatively less often, this causes less reconciliation at a high than at a low aggression intensity. Furthermore, due to the fact that the spatial structure is relatively more rigid at a high aggression intensity, individuals are more often close to the same partner and this increases the chance that they are close to a

former opponent at all times. Therefore, the frequency with which individuals groom with former opponents sooner after a fight than in the matched control (MC-PC method) declines. This reduces the rate of reported reconciliation. Besides, due to the relatively rigid spatial structure at a high aggression intensity, individuals more often reconcile with the same partners as they groom with and thus, they reconcile with valuable partners more often than at a low aggression intensity. In sum, aggression structures the spatial configuration of individuals in the group and (together with grooming out of fear of defeat) this structures the affiliative patterns.

Relevance to empirical data

Although in empirical data rank is not measured by an internal Dom value (like in our model), similar results were obtained in the model if rank was computed by the empirical measure, the average percentage of winning (Hemelrijk et al. 2005). In the model, the correlations with rank and 1) aggression given, 2) aggression received and 3) fights lost appeared to be stronger at a high intensity of aggression than at a low one (10-12 in Table 6). Whether this difference may serve as a new indication of the degree of despotism for real primates needs further study (2-4 Table 2C).

The relevance of the model to affiliative patterns of primates is supported by the following empirical evidence (Table 2). First, in many species grooming up the hierarchy appears to be stronger the steeper the gradient of the hierarchy when comparing between groups of a single species (Schino & Aureli 2008b) (conform 3 in Table 2A). Further, the larger inter-individual distance at high versus low aggression intensity in the model (6 in Table 2C) is confirmed in empirical data at several levels of comparison, not only by a comparison between species, namely between rhesus and tonkean macaques (Thierry 1990), and between rhesus and stump-tailed macaques (de Waal & Luttrell 1989) (see Table 1), but also within groups intense conflicts result in larger distances between opponents than do mild conflicts in both a group of Japanese macaques (Majolo et al. 2009) and wild chimpanzees (Arnold & Whiten 2001). The correlation between proximity and

grooming (1 in Table 2A) is supported in lion-tailed macaques and tonkean macaques (Thierry et al. 1990; Singh & Krishna 2006) and by the difference in distance and grooming frequency between despotic rhesus monkeys and egalitarian stump-tailed macaques (de Waal & Luttrell 1989). The combination of spatial configuration and proximity induced grooming leads to reciprocity of grooming. This mechanism may underlie the so-called 'symmetry-based' reciprocity (de Waal 2000) where the correlation results from a common underlying variable, namely proximity.

As to the extent to which closer proximity between former opponents after a fight explains the occurrence of the higher grooming tendency after a fight (which is interpreted as reconciliation), a number of empirical studies confirm this. These studies concerned stump-tailed macaques, rhesus macaques (Call 1999; Call et al. 1999), Japanese macaques (Majolo et al. 2009), Moor macaques (Matsumura 1996) and a comparison between studies of several species in captivity vs. natural conditions (Sommer et al. 2002).

However, a number of studies conclude that closer distance after a fight cannot explain the conciliatory tendency exhaustively, because when controlling for distance by matching (to some degree) the distance in the matched control to that after the fight (in the post conflict period), these studies show that a certain conciliatory tendency still remains after controlling for distance (Petit et al. 1997; Swedell 1997; Kutsukake & Castles 2001; Majolo et al. 2005; Majolo & Koyama 2006; Cooper et al. 2007) despite a great reduction in the conciliatory tendency in some studies (Call 1999). In the model, conciliatory tendency is also reduced when controlling for proximity during the MC period. However, whether it disappears or it is only reduced depends on the distance of proximity controlled during the MC (see chapter 7).

Further, as in the model (21 in Table 6; 1 in Table 2B), females of a group of baboons reconciled more often with higher ranking victims than lower ranking ones (Silk et al. 1996). In the model, this arises at a high aggression intensity, because individuals groom others of higher rank more often, since they are afraid to attack

them. Thus, they also groom high ranking ones after a fight more often and thus reconcile with others of higher rank more. Note that this finding also may be interpreted in the frame of the most valuable relationship hypothesis, because the higher the rank of the partner (due to the effective support it can give, for instance) the more valuable the individual is to reconcile with.

Further, as in the model, a correlation between rank and grooming is lacking (2 in Table 2A) in the study of baboons and vervets (which are despotic species) (Seyfarth 1976; Seyfarth 1980), but such a correlation is found in lion tailed macaques (in this study this species appears to be despotic) (Singh & Krishna 2006). Since the absence of this correlation in the model is due to spatial centrality of dominants, we expect spatial social structure to be stronger in baboons and vervets than in lion tailed macaques.

At a high intensity of attack, but not at a low one, lower ranking females are more anxious (5 in Table 6; 12 in Table 2C), because they more often receive aggression and lose fights than higher ranking individuals in the model (10-12 in Table 6; 3-4 in Table 2C). This is confirmed by correlations between the frequency of receipt of aggression, the level of anxiety, and anxiety-induced arthrosclerosis in the fiercely aggressive despotic macaque species, rhesus and long-tailed macaques (Shively 1998; Kaplan & Manuck 1999; Abbott et al. 2003). It is of interest to see whether in empirical data, like in the model (5 in Table 6) this correlation between rank and anxiety is weaker in egalitarian species (12 in Table 2C).

Thinking along the lines of dominance relations, our model may also change our explanations for two other phenomena. Firstly, in female-bonded species, in primate groups that are more female-biased females appear to groom less frequently. This is explained by the assumption that in female-bonded groups not every female needs to groom every other (Lehmann et al. 2007). According to our model, however, reduced grooming by females in a group that is female-biased may be a side-effect of the rule that individuals groom the others out of fear of defeat: Because in a female-biased group females meet other females more often and they fear defeat less if they meet a female than if they meet a male, they will

attack more than in a group with more males. Second, the fact that female macaques groom males more often than vice versa (Estrada & Sandoval 1977; Koyama 1984; Kurup 1988; Thierry et al. 1990; Tsukahara 1990) is explained by our model as a consequence of their subordinance to males. From this we may derive another prediction: since in despotic species females are dominant over a higher number of males than in egalitarian species (Hemelrijk et al. 2008a), we expect that (for the same adult sex ratio in despotic and egalitarian groups) females of despotic species groom males less than females of egalitarian species do (13 in Table 2C).

Shortcomings and benefits of our model

Our model shows the four different levels of complexity of social behaviour distinguished by Hinde (1982): Individual behaviour, interactions, relationships, and social structure. In agreement with Hinde'suggestion, each level can be described in terms of the level below it, and levels influence each other mutually. For instance, the nature of the behaviour of the participants influences their relationship and these relationships in turn, also influence the behaviour of the participants. Also related to this view is that observed social structure can vary dramatically with circumstances, without any changes in the underlying motivational mechanisms or strategies. For instance, here we show that patterns of reconciliation differ depending on intensity of aggression and in our former paper we showed that female dominance increases with the percentage of males in the group (Hemelrijk et al. 2008a).

A criticism made against DomWorld by Bryson and co-authors (2007) has been that the dominance hierarchy in the model was not as stable as that of real primates. The dominance hierarchy in GrooFiWorld is stable, however, because average dominance values between periods 200 and 230 are significantly correlated with those between 231 and 260 (see methods). Further, in GrooFiWorld we have shown that even if we keep the hierarchy 100% stable (by omitting the self-reinforcing effects of winning and losing fights) all patterns remain similar (Table 4, 5).

Another criticism concerned the directional inconsistency of aggression (de Vries 2009). The directional inconsistency of aggression at high aggression intensity in DomWorld appeared to be lower than that in empirical data. In the present paper, in GrooFiWorld, the directional inconsistency is higher than in DomWorld. 0.73 vs 0.55 respectively, because in GrooFiWorld the individuals think twice before they attack, whereas in DomWorld they think only once and thus, attack higher ranking individuals more often. How it compares exactly to empirical data is not clear, because the matrices tested by de Vries sometimes comprise of males, sometimes of females and sometimes of both sexes and the directional inconsistency probably depends on the group composition. However, despotic macaque species show an average directional inconsistency of 0.89, which still is above that of GrooFiWorld. To study this in more detail is beyond the scope of this paper.

Yet, there are other shortcomings in our study of the model that will be amended in future. There are a number of patterns related to reconciliation that have been found in studies of real primates that we do not yet treat in the model (Silk et al. 1996; Silk 1997; Silk 1998; Silk 2002b; Silk 2007a; Romero et al. 2009), we used the time rule method (Aureli et al. 1989) neither to test for reconciliation nor for the valuable relationship hypothesis, nor did we control for proximity in our study of reconciliation (but see chapter 7). The rule of grooming out of fear of defeat may be interpreted by assuming that individuals groom others to calm these partners down and to forestall the chance of receiving aggression from them; thus, it could be viewed as an exchange of grooming for tolerance. However, in the present model grooming others does not influence whether or not the groomee will subsequently attack the groomer. The model also does not represent cases in which grooming can be rejected by the receiver, nor pre-existing differences between individuals, such as are apparent, for instance, between primates of different personality (Capitanio 2004), nor what individuals compete for such as sex or food. It omits kin-relations and offspring among partners as well as coalitions. Besides, we have not yet studied effects of different sex ratios, whereas primate groups of the same species may differ in sex ratios, and this has been shown to

have an influence on their affiliative patterns (Hill 1990; Hemelrijk & Luteijn 1998; Hill 1999; Lehmann et al. 2007). These are natural variations and extensions that will need to be added to our model, as we intend to do in future studies.

As to cognition, our model does not at all reflect the behavioural and cognitive complexity of primates. Regarding affiliation, it is confined only to the representation of an anxiety reducing effect of grooming in the context of a competitive regime. Because of the resemblance of the emergent affiliative patterns in our model to those of primates, similar processes may cause these affiliative patterns in primates also. Whether or not primates may (sometimes) use the more complex cognitive rules that have been suggested by primatologists before, our model cannot decide. Instead, our model may be used as a null-model that indicates what patterns we should expect in the absence of the usual cognitive rules regarding reciprocation, reconciliation, etcetera. Thus, it does not deny that primates are intelligent as has been shown in many experimental studies (Premack 1988; Tomasello & Call 1997; Cheney & Seyfarth 2007), but it questions whether these primates use all aspects of their intelligence in all contexts. It illustrates that apart from the here reproduced patterns at a group level in the model, extra evidence, is needed as proof of 1) intentional reciprocation, 2) competition for higher ranking grooming partners, and 3) intentional exchange and 4) intentional reconciliation. Further, our model points to the need for more studies of the spatial distribution of monkeys within a group. Of these studies (Itani 1954; Rasmussen & Farrington 1994) (Girod, Thierry, Hemelrijk, in prep), there have been only a few so far.

In sum, we have shown that without the specific cognitive assumptions for the creation of each pattern of grooming, cognitively simple local interactions and self-organization suffice to produce many of the affiliative patterns that are typical of egalitarian and despotic primate societies (Table 1, 4) and also a number of other patterns (Table 6). The main finding is that the spatial configuration associated with the competitive regime and grooming out of fear of defeat or out of anxiety structure the patterns of grooming such that we measure patterns of reciprocation, exchange and reconciliation. This leads to a number of model-based hypotheses for

real primates (Table 2). Because the model generates many of the behavioural patterns found in real primates, but does so without the usually assumed cognitive processes, it can be used as a null model for studying primate affiliative behaviour.

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Chapter 3

An Individual-Oriented Model on the Emergence of Support in Fights, its Reciprocation and Exchange

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Abstract

Complex social behaviour of primates has usually been attributed to the operation of complex cognition. Recently, models have shown that constraints imposed by the socio-spatial structuring of individuals in a group may result in an unexpectedly high number of patterns of complex social behaviour, resembling the dominance styles of egalitarian and despotic species of macaques and the differences between them. This includes affiliative patterns, such as reciprocation of grooming, grooming up the hierarchy, and reconciliation. In the present study, we show that the distribution of support in fights, which is the social behaviour that is potentially most sophisticated in terms of cognitive processes, may emerge in the same way. The model represents the spatial grouping of individuals and their social behaviour, such as their avoidance of risks during attacks, the self-reinforcing effects of winning and losing their fights, their tendency to join in fights of others that are close by (social facilitation), their tendency to groom when they are anxious, the reduction of their anxiety by grooming, and the increase of anxiety when involved in aggression. Further, we represent the difference in intensity of aggression apparent in egalitarian and despotic macaques. The model reproduces many aspects of support in fights, such as its different types, namely, conservative, bridging and revolutionary, patterns of choice of coalition partners attributed to triadic awareness, those of reciprocation of support and 'spiteful acts' and of exchange between support and grooming. This work is important, because it suggests that behaviour that seems to result from sophisticated cognition may be a side-effect of spatial structure and dominance interactions and it shows that partial correlations fail to completely omit these effects of spatial structure. Further, the model is falsifiable, since it results in many patterns that can easily be tested in real primates by means of existing data.

Introduction

When observing complex behaviour of animals, we automatically attribute it to sophisticated cognitive mechanisms. This is usually accepted when observing intelligent animals, such as primates and humans (de Waal & Ferrari 2010), but not in the case of social insects, when we study, for instance, the complex organization of their large colonies (Seeley 1995) or the highly sophisticated architecture of their nests, such as termite hills (Turner 2000). The cognitive complexity of insects is known to be limited and, therefore, complexity of traits is thought to arise by self-organization (Camazine et al. 2001; Hemelrijk 2002). However, more recently, complex traits in taxa with great cognitive sophistication have also increasingly been considered to be due to self-organization based on cognitively simple behavioural rules (Hutchinson & Gigerenzer 2005; Shettleworth 2010; Hemelrijk & Bolhuis 2011). This even includes patterns of behaviour in humans, such as the segregation of races (Schelling 1978) and the complexity of financial markets (Farmer et al. 2005). This means that it is difficult to tell what part of the complex spontaneous behaviour of highly intelligent animals, such as primates, is due to cognitive sophistication and what part is due self-organization (Hemelrijk 1996b).

In the present paper, we demonstrate in a computer model that among agents with minimal cognition, patterns of coalitions emerge from grouping, dominance interactions, and grooming through self-organization. These cognitively simple agents appear to form coalitions, show patterns usually thought to indicate triadic awareness in the choice of coalition partners, and reciprocate support in fights and exchange it for grooming.

More than any other behaviour, coalition formation has been thought to reflect the cognitive sophistication of primates (Harcourt & de Waal 1992). Recruitment of support is believed to involve awareness of the social relationships between other individuals in connection with the relations between the individual itself and these other individuals, so-called ‘triadic awareness’ (Harcourt & de Waal 1992; Gore 1994; Silk 1999; Perry et al. 2004; Schino et al. 2006; Cheney & Seyfarth 2007; Paxton et al. 2010). Support in fights and grooming have been regarded as altruistic and according to the framework of reciprocal altruism, their receipt

should be repaid in return (Trivers 1971) by cognitively keeping track of the number of acts given to, and received from each partner, so-called calculated reciprocity (de Waal & Luttrell 1988; Frank & Silk 2009; Gomes & Boesch 2009). Calculated reciprocity was suggested to be most complicated in cases where individuals reciprocated not only their support but also their opposition towards others (called contra-support), showing so-called spiteful behaviour (de Waal & Luttrell 1988).

The necessary involvement of sophisticated cognitive abilities in reciprocation is a point of view that is not adhered to by all scientists. For example, Range and Noë (Range & Nöe 2005) argue that in recruiting support, individuals may simply recruit others of higher rank than themselves and no triadic awareness is needed. Stevens and colleagues (Stevens & Hauser 2004; Stevens et al. 2005; but see Dufour et al. 2009) contend that food sharing reflects tolerated theft (Stevens & Cushman 2004) and that calculated reciprocity has so far not been shown (Stevens & Gilby 2004). Others suggest that coalition behaviour may involve simple rules of thumb (Bissonnette et al. 2009), that its reciprocation and exchange may emerge as a side-effect from opportunistic attacks (Hemelrijk & Ek 1991; Prud'homme & Chapais 1996; Widdig et al. 2000) or involve a kind of emotional book-keeping (Schino & Aureli 2009) and that chimpanzees are not able to show spiteful behaviour, but that they merely retaliate (Jensen et al. 2007). In agreement with this, animal taxa with supposedly lower cognitive abilities, such as hyenas, appear to show patterns of coalition behaviour and reciprocation similar to primates (Smith et al. 2010).

In our study, we avoid this debate on what intelligence underlies complex social behaviour in primates. Instead, our study is part of a broader research program, in studies of humans and animals, also called the 'low-intelligence approach' (Farmer et al. 2005) or that of 'minimal cognition' (Hemelrijk & Bolhuis 2011), in which 'null-models' are developed for complex patterns of behaviour. We use an earlier computer model (Puga-Gonzalez et al. 2009) to investigate whether patterns of coalition, such as reciprocation of support and the exchange between support and grooming, may result through self-organization due to aversion of risks of attack, anxiety-reducing effects of grooming and socio-spatial structuring. We

give individual agents 'minimal cognition': individuals aggregate and when they are too close to others, they are more likely to attack them if they are under the impression that they will win (Hemelrijk 1999a; Hemelrijk 2000a). Winning and losing has self-reinforcing effects (Mendoza & Barchas 1983; Barchas & Mendoza 1984; Chase et al. 2002; Hemelrijk et al. 2008a). However, when individuals fear defeat, they will tend to groom the other individual, particularly when they are anxious (Puga-Gonzalez et al. 2009). Coalitions may emerge in the model as a consequence of 'social facilitation', i.e., an individual C close to a fight is activated sooner than another individual that is further away. Such spatial proximity (e.g., C being close to the two combatants, A and B, Figure 1) may incidentally result in support in the fight when an individual (C) attacks one of two combatants (e.g., B), because this is counted as an act of support (for A) and opposition (to B)(also called contra-support), as is done when recording behaviour of real primates (Silk 1982; Hunte & Horrocks 1987; de Waal & Luttrell 1988; Hemelrijk & Ek 1991; Silk 1992; Widdig et al. 2000; Silk et al. 2004; Cooper et al. 2005; Widdig et al. 2006; Berman et al. 2007; Schino et al. 2007). In the present paper, we will refer to contra-support by the word 'opposition'.

In our present study, we first derive predictions for our model by means of a survey of empirical patterns of coalition (Table 1). Primate species have been shown to differ in dominance style or type of society, often classified as egalitarian and despotic, with different gradations (Vehrencamp 1983; Thierry 2004). Since dominance style has been shown to influence patterns of both aggression and grooming (Thierry 2004; Thierry et al. 2008; Balasubramaniam et al. 2012a), we also study the relationship between dominance style and coalitions in the model. In primates, the most detailed comparison between despotic and egalitarian species has been made in the genus of macaques. Here, despotic species differ from egalitarian ones in several traits: they have a steeper hierarchy, lower frequency of aggression, more asymmetrical aggression, greater dominance of females over males (Hemelrijk et al. 2008a), a lower conciliatory tendency (Thierry 2004; Thierry et al. 2008), and more grooming up the hierarchy and of others of similar rank (Puga-Gonzalez et al. 2009).

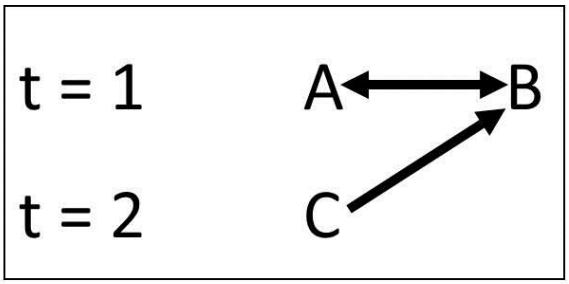

Fig 1. Coalitions in GrooFiWorld. At time 1, individuals *A* and *B* are fighting. At time 2, individual *C* attacks *B* and hereby supports *A* and opposes *B* (contra-support). Individual *C* is the supporter and individual *B* is the target.

We have shown in earlier studies that this modelling approach produces both the patterns of aggression, grooming and conciliatory behaviour exhibited by many primate species and the differences between egalitarian and despotic species of macaques (Hemelrijk 1999a; Hemelrijk et al. 2008a; Puga-Gonzalez et al. 2009; Hemelrijk & Bolhuis 2011), while in our present study, we demonstrate that these findings still hold for a larger group size (of 30 instead of 12 individuals) (Puga-Gonzalez et al. 2009). Furthermore, we show that such an approach also leads to surprisingly good predictions regarding new patterns: different types of coalitions, i.e., conservative, bridging or revolutionary coalitions (Chapais 1992), indications of triadic awareness in the choice of coalition partners, reciprocation of support and opposition and exchange between support and grooming. We deliver predictions to verify our findings.

Methods

Survey of empirical data.

To compare the results of the model to empirical data, we surveyed the literature on coalitions in primates (Table 1). We confine ourselves to adults and to Old World primates, because New World primates differ in their patterns of social interactions, e.g., in the percentage of the time spent grooming and in their patterns of

grooming (Dunbar 1991; Ahumada 1992; Obrien 1993; Parr et al. 1997). We only included studies of coalition patterns among individuals of the same sex. We surveyed 26 studies, comprising 31 groups of 13 different species (Table 1).

The model

In our model, called GroofiWorld (Puga-Gonzalez et al. 2009), we represent the essential traits of primate societies: individuals group and they compete in the group for unspecified reasons. In this competition, the effects of winning and losing are self-reinforcing (Mendoza & Barchas 1983; Barchas & Mendoza 1984; Eaton 1984; Hsu et al. 2006) and individuals try to avoid the risk of losing a fight (Popp & DeVore 1979). When risks are high, individuals will tend to avoid the risk of losing a fight by grooming the other individual instead. Thus, individuals first consider fighting and then grooming. This order is based on the observation by Kummer that unfamiliar individuals will first fight with each other and then groom (Kummer 1974). Individuals in the model become more anxious after a fight, as indicated in reality by the increase in frequency of scratching and heart rate in both opponents (Aureli et al. 1989; Aureli & van Schaik 1991; Aureli 1992; Aureli 1997; Castles & Whiten 1998; Das et al. 1998; Silk 2002b; Cooper et al. 2007). In addition, in the model, their anxiety may subsequently be reduced by the receipt of affiliative behaviour and, to a lesser degree by active grooming, as indicated by the reduced heart rate and the drop in the rate of self-directed behaviour in many species (Aureli & van Schaik 1991; Castles & Whiten 1998; Das et al. 1998; Aureli et al. 1999; Shutt et al. 2007). Furthermore, our model is informed by empirical studies on grooming and opiate administration which indicate that not being groomed for some length of time reduces the concentration of endorphins and increases the motivation to be groomed, and that grooming increases the level of endorphins in the brain and reduces the motivation to groom (Meller et al. 1980; Fabre-Nys et al. 1982; Keverne et al. 1989; Schino & Troisi 1992; Martel et al. 1995; Graves et al. 2002). Individuals are activated in random order, but if an individual is close to a fight, i.e., within a certain radius (see Table 2 for radius of social facilitation), then it may be activated earlier, i.e., through social facilitation (Table 2). We refer to

Table 1.

Species	Dominance style	# Subjects (Group size)	% Fem in group	Coalitions as % of fights	% of coalition types	Reciprocity of support	Exchange of: Grooming for support	Exchange of: Support for grooming	Reciprocity of opposition	Sources
1) *M. sylvanus*	[1]E	51(250)	--	--	--	--	--	--	--	(Prudhomme & Chapais 1993)
2) *M. radiata*	[1]E	10(72-80)	80%	--	R:9%	[2]NO	NO	--	--	(Silk 1982)
3) *M. assamensis*	[1]D	10(64)	52%	15%	--	--	[3]YES	--	--	(Cooper et al. 2005; Cooper & Bernstein 2008)
4) *M. fascicularis*	[1]D	21(30-40)	--	--	--	--	YES	--	--	(Hemelrijk 1994)
5) *M. fuscata*	[1]D	18(37)	--	6%	C:70% B:26% R:4%	--	--	--	--	(Vasey 1996)
6) *M. fuscata*	[1]D	Nina group: 8(25)	--	--	--	--	--	YES	--	(Ventura et al. 2006)
7) *M. fuscata*	[1]D	Kw group: 20(55)	--	--	--	--	--	YES	--	(Ventura et al. 2006)
8) *M. fuscata*	[1]D	23(57)	--	6%	--	YES	YES	YES	--	(Schino et al. 2007)
9) *M. mulatta*	[1]D	12(?)	--	--	--	--	YES	--	--	(Kapsalis & Berman 1996)
10) *M. mulatta*	[1]D	34(172)	53%	--	--	--	--	--	--	(Widdig et al. 2006)
11) *C. aethiops*	NA	Group A: 8(29)	53%	--	--	--	YES	--	--	(Seyfarth 1980)
12) *C. aethiops*	NA	Group B: 7(17)	70%	--	--	--	NO	--	--	(Seyfarth 1980)
13) *C. aethiops*	NA	Group C: 8(29)	66%	--	--	--	YES	--	--	(Seyfarth 1980)

Table 1. cont.

Species	Dominance style	# Subjects (Group size)	% Fem in group	Coalitions as % of fights	% of coalition types	Reciprocity of support	Exchange of: Grooming for support	Exchange of: Support for grooming	Reciprocity of opposition	Sources
14) *P. cynocephalus*	NA	Linda: 11(NA)	--	4%	C:76%	[2]NO	[2]NO	--	--	(Silk et al. 2004)
15) *P. cynocephalus*	NA	Nyayo: 17(NA)	--	1%	C:76%	[2]NO	[2]NO	--	--	(Silk et al. 2004)
16) *P. cynocephalus*	NA	Omo: 7(NA)	--	3%	C:76%	[2]NO	[2]NO	--	--	(Silk et al. 2004)
17) *P. cynocephalus*	NA	Viola: 10(NA)	--	3%	C:76%	[2]NO	[2]YES	--	--	(Silk et al. 2004)
18) *P. cynocephalus*	NA	Weaver: 14(NA)	--	2%	C:76%	[2]YES	[2]NO	--	--	(Silk et al. 2004)
19) *P. cynocephalus*	NA	8(24)	80%	7%	--	YES	--	--	--	(Seyfarth 1976, reviewed in Smith et al. 2010)
20) *P. hamadryas ursinus*	NA	13(70)	75%	4.4/10.5[4]	--	--	--	--	--	(Wittig et al. 2007)
21) *T. gelada*	NA	3-6(NA)	--	--	--	YES	--	--	--	(Dunbar 1980)
22) *P. troglodytes*	NA	16(20-30)	64%	--	--	YES	YES	YES	NO	(Hemelrijk & Ek 1991)

Table 1. Coalition patterns among adult females in Old-World primates. Coalition types: C:Conservative, B:Bridging, R:Revolutionary (Chapais 1992). NA: not available. --: not tested. [1](Thierry 2004). [2]Only partial Tau-Kr value reported. [3]Calculated here using published data. [4]Physical support/physical and vocal support.

chapter 2 in this thesis for more details of the model. Below, we describe the way in which coalitions were recorded in the model, how parameters were set, and analyses and experiments were carried out.

Coalitions

If two individuals attack the same target in two subsequent activations, this is classified as an event of coalition and opposition (Fig 1).

Parameters

Where possible, we kept the parameters of the model (Table 2) the same as in our previous studies (Hemelrijk et al. 2003; Puga-Gonzalez et al. 2009). However, in order to also study interaction patterns among males in the future (Puga-Gonzalez et al, in prep), and given that the number of males in primate groups is lower than that of females, we used a larger group size to reach the minimal sample size of four that is required for the statistical analysis of males. Empirical studies show that the percentage of males in groups is approximately 30% in egalitarian primates and approximately 20% in despotic primates (Caldecott 1986; Ménard 2004; Wantia 2007). Therefore, our group size of 30 individuals included 21 females and 9 males at low intensity and 24 females and 6 males at high intensity. As a consequence of increasing the group size to 30 individuals, one empirical pattern was no longer met: the percentage of time spent fighting among females was no longer lower at high intensity of aggression when compared to low intensity of aggression (de Waal & Luttrell 1989; Thierry 2004). We solved this problem by increasing the risk-aversion of an individual, *RiskAvers,* when its opponent's intensity of aggression was higher (Equation 1). Consequently, the percentage of time spent fighting was lower at high intensity of aggression than at low intensity of aggression, in accordance with empirical data. Here, the average number of 'mental' battles at high intensity of aggression was ~2 and at low intensity, ~1.

$$RiskAvers = 2^{IntensityAggressionOpponent} \quad (1)$$

Parameter	Description	Females	Males
General Parameters			
GroupSize	Total number of individuals	30	
Sex ratio (at high aggression intensity)	Number of	24	6
Sex ratio (at low aggression intensity)	Number of	21	9
InitRadius	Predefined space at start of simulation	1.7*# Inds	1.7*# Inds
Radius of social facilitation	Radius starting from centre point between two opponents	10	10
Grouping Parameters			
PersSpace	Close encounter distance	8	8
NearView	Medium distance	24	24
MaxView	Maximal viewing distance	50	50
SearchAngle	Turning angle to find others	90°	90°
VisionAngle	Angle of field of view	90°	90°
Dominance Parameters			
InitDom	Initial Dom value	16	32
RiskAvers (high intensity)	Number of 'mental battles'	~2 (Eq. 1)	~2 (Eq. 1)
RiskAvers (low intensity)	Number of 'mental battles'	~1 (Eq. 1)	~1 (Eq. 1)
StepDom (high intensity)	Scaling factor for aggression intensity	0.8	1
StepDom (low intensity)	Scaling factor for aggression intensity	0.08	0.1
FleeingDistance	After losing a fight	2	2
ChaseDistance	After winning a fight	1	1
Grooming Parameters			
InitAnx	Initial anxiety value	0.5	0.5
AnxInc	Increase in anxiety after every activation	1%	1%
AnxDcrGree	Decrease of anxiety of groomee	0.15	0.15
AnxDcrGrmr	Decrease of anxiety of groomer	0.1	0.1
AnxIncFight	Increase of anxiety after fighting	0.1	0.1

Table 2. Default parameter values in 'GrooFiWorld'

Experimental set-up

We performed four experiments to understand what caused the patterns of coalition in the model. First, we switched off 'social facilitation' (i.e., the shortening of the waiting-time of those individuals close to a dominance interaction). Thus, when social facilitation is off, individuals close to a fight are as likely to be activated next as any other individual. Second, we disabled rank differences among individuals by randomly shuffling Dom values among all individuals after every activation. We used fixed Dom values (thus switching off the self-reinforcing effects). We took these Dom values for the corresponding intensity of aggression from the middle of the interval in which the Dom values were considered to have stabilized, thus, from between periods 200 and 260 (i.e., period 230) (Hemelrijk & Gygax 2004). Third, we investigated the role of non-random spatial structure by making individuals interact with randomly chosen partners. Fourth, we investigated the role of the combination of spatial structure and rank by disabling them simultaneously. See Table 1 in appendix further experimental manipulations of the behavioural rules (taking out the effect of anxiety on grooming, adjusting the probability of attacking other individuals to 28% at high intensity and 42% at low intensity (percentages are adjusted such that the same percentage of fights results as in the full model), independent of the risks involved, and reversing the order of behavioural rules concerning aggression and grooming and randomizing the order).

Data collection and analysis

Every run consisted of 260 periods and each period consisted of 600 activations (i.e., GroupSize times 20). Data were collected from period 200 to 260 to exclude any bias caused by transient values. Data consisted of spatial position and direction of each individual and, for coalitions, fights and grooming behaviour of: 1) the actor and receiver and of the winner and loser and 2) the Dom values and degree of anxiety. For each condition (the complete model, and the models without one or more assumptions), 10 independent replicas were run for each of the two aggression intensities (high and low). The results are shown as the average value of the statistic over 10 runs for each condition. Their combined probability is based on

the improved Bonferroni procedure (Hochberg 1988). We used non-parametric statistics and two-tailed probabilities. We only used one-tailed probabilities if patterns were predicted by empirical studies.

The percentage of time individuals spend fighting (or grooming) was calculated by dividing the total number of fights (or grooming bouts) by the total number of activations. Similar to empirical studies, the percentage of coalitions was calculated as the total number of coalitions divided by the total number of fights (Silk et al. 2004; Schino et al. 2007).

The rank of group members was calculated as the average Dom value for each individual per run over periods 200-260. We used an average measure because we correlated it with an average measure of aggressive and affiliative acts, i.e., data were summed over the whole interval of period 200-260.

The hierarchical differentiation among individuals was measured by the coefficient of variation of Dom values for the average rank of each individual over period 200-260 and this was averaged over 10 runs. Higher values indicate greater rank distances between individuals (Hemelrijk 1999a). Hierarchical differentiation is also reflected in the empirical behavioural measure of the degree of unidirectionality of aggression, which we present as well (Hemelrijk 1990a; Thierry 2004).

The degree to which dominant individuals of a certain sex occupy the centre of the group was measured by a correlation between an individual's average Dom value and the average spatial direction of others around it. The centrality of each individual is calculated by means of circular statistics by drawing a unit circle around 'ego' and projecting the direction of other group members as points on the circumference of this circle (Mardia 1972). The connection of these points with ego's location results in vectors. The length of the average vector represents the degree to which group members form a cluster relative to ego. Thus, longer mean vectors indicate a more peripheral, and hence, less central location of ego. The centrality of dominants is therefore represented by a negative correlation between rank and the length of the average vector (indicating the average direction of other individuals).

Correlations between the distribution of grooming, aggression, support and opposition among individuals, and between social interactions and rank and proximity were computed by means of the Tau-Kr correlation, as described by Hemelrijk (1990a; 1990b). Matrices of support (and opposition) were corrected for opportunity (number of fights) to support (or oppose) each partner. Matrices of proximity were constructed using the average distance between individuals. All matrices were based on data collected over the supposedly stable periods from 200 to 260. The level of significance was calculated using 2000 permutations (Hemelrijk 1990a; Hemelrijk 1990b). We tested for reciprocity and exchange of attack, grooming, support and opposition by correlating an actor and receiver matrix with the Tau-Kr correlation (Hemelrijk 1990b). To compare our results to those for real primates, we investigated the possibility that correlations were a side-effect of a correlation with a third variable by partialling it out using partial Tau-Kr correlations (Hemelrijk 1990a). The third variables concerned rank and proximity.

Whether social behaviour (i.e., grooming, aggression, support and opposition) was directed up the hierarchy or towards partners of similar rank was computed, respectively, using the Tau-Kr correlation between the matrix of social behaviour and the matrix of the rank of partners (with the average Dom values of partners in the rows) and the matrix of partners of similar rank (filled with zeros apart from the partners closest and second closest in rank, which are indicated as 1's). Note that higher-ranking individuals have higher Dom values. Thus, a significant positive correlation corresponds to social behaviour being directed up the hierarchy and towards individuals of similar rank, respectively.

Because of the high number of correlations, significant results may arise by chance. We corrected for this in two ways. We used the Bonferroni correction and discarded the 5% of the lowest significances (Type I error) per table of results.

Results

Empirical patterns

In our survey of the empirical literature on coalitions in primates, we focus on females because they have been studied more often than males (in 22 studies versus 14 studies on males).These results serve as predictions for our models. Our survey shows that, on average, adult females form coalitions in 5% of their fights (based on 10 studies, Table 1), that these coalitions are most often conservative (all-down), less often bridging and least often revolutionary (all-up, 16-18 in Table 3), and that they reveal patterns that have been attributed to triadic awareness in the choice of coalition partners (19-21 in Table 3). This is inferred when individuals solicit support from others that are higher in rank than either they, themselves, or their opponent, even if the solicitor ranks below the opponent (Perry et al. 2004; Schino et al. 2006), and when individuals (independent of their rank relative to the opponent) solicit support from others with a better relationship with them than with their opponent (Perry et al. 2004; Schino et al. 2006). Further, adult females reciprocate support at a group level in 50% of the studies (5/10), or 100% when excluding the studies based on partial correlations (namely studies by Silk 1982; Silk et al. 2004), they exchange support for receipt of grooming in 100% (4/4) of the studies and they groom for receipt of support in 57% (8/14) (or 78% when excluding partial correlations: (Silk et al. 2004)) of the studies (Table 1). Reciprocation of opposition was tested among adult females in a single study only, namely in chimpanzee females, and appeared to be absent (Hemelrijk & Ek 1991). Whether results differ between dominance style, i.e., egalitarian and despotic, cannot be tested due to the small sample size.

Analysis of empirical coalition patterns in the model

With reference to the *percentage of fights* with coalitions, the model generates percentages of incidental support that resemble those in real primates if vocal coalitions are included (13 in Table 3), despite the absence of any rules for coalition-formation. Furthermore, the percentages are higher than those for

empirical data from which vocal coalitions have been excluded (Mann-Whitney U: high intensity vs empirical data, n_1=10, n_2=9, U=80, p<0.01; low intensity versus empirical data, n_1=10, n_2=9, U=79, p<0.01). As is the case for empirical data, coalitions in the model appear to be triadic more often than polyadic, but the percentage of triadic coalitions (96% - 98%, 14 in Table 3) is higher than for empirical data, at 75%, and that of polyadic coalitions is lower, at 2-4%, in the model than for empirical data, at 25% (15 in Table 3) (de Waal & Harcourt 1992).

At high intensity of aggression in the model, *coalition types* are most often conservative, sometimes bridging, and least often revolutionary (16-18 in Table 3), while at low intensity of aggression, coalitions are usually revolutionary and less often conservative or bridging (Mann-Whitney U test, n=10; revolutionary vs conservative: U=100 p<0.01; revolutionary vs bridging: U=100, p<0.01; conservative vs bridging: U= 63, p>0.1). In relation to *triadic awareness* of the choice of coalition partners (19 in Table 3), despite the absence of soliciting behaviour in our model, supporters appear mostly to be higher in rank than the receiver (i.e., the individual that could have solicited) and also than the target at high intensity of aggression, even if the receiver ('solicitor') ranks below its opponent. This resembles pooled empirical data for individuals of both sexes in studies on capuchin monkeys and Japanese macaques (Perry et al. 2004; Schino et al. 2006). Further, in agreement with empirical data, the relationship of the supporter - measured by the sociality index of Perry and co-authors (Perry et al. 2004)- is better with the receiver ('solicitor') than with the target in the model at both intensities (20, 21 in Table 3).

Females *reciprocate* support and *interchange* grooming for receipt of support and support for receipt of grooming at both intensities of aggression in the model (22-24 in Table 3). This resembles empirical data, but reciprocation of support and exchange of grooming for support are found at a higher frequency (100% vs 50% and 100% vs 57% respectively) in the model.

Supporting a certain individual in a triadic fight implies opposing the other individual. *Opposition* is reciprocated at low intensity of aggression (thus, individuals more often oppose those partners from whom they receive more opposition (Hemelrijk 1990a)) but not reciprocated at high intensity of aggression,

Table 3.

	Empirical studies on macaques		GrooFiWorld	
Intensity of Aggression	Despotic	Egalitarian	High	Low
Dominance Style				
1) Gradient of the hierarchy (CV)[1]	NA	NA	0.72	0.36
Gradient of the hierarchy High > Low	NA		U=100***	
2) Unidirectionality of Aggression (TauKr)	[2]True	[2]NS	-0.13**	0.51***
Unidirectionality of aggression High > Low	[2]True		U=100**	
3) Time spent fighting (%)	[2]NA	[2]NA	13 %	17 %
Fighting % High < Low	[2]NA		U=100***	
4) Relative female dominance	[3]0.23	[3]0.00	0.22	0.00
Relative female dominance High > Low	[3]True		U=100***	
5) Average distance among all group members	[2]High	[2]Low	29	25
Average distance High < Low	[2]NA		U=97***	
6) Centrality of Dominants (Tau)	[2]True	[2]NA	-0.40**	-0.10
Centrality High > Low	[2]NA		U=100***	
Affiliative patterns				
7) Time spent grooming (%)	[2]8-15	[2]NA	17	20
8) Conciliatory Tendency	[2]7-18	[2]20-50	21	31
Conciliatory tendency High < Low	[2]U=66*		U=100***	
9) Grooming Reciprocation (TauKr)	[2]True	[2]True	0.39***	0.54***
Grooming Reciprocation High < Low	[2]NA		U=94***	
10) Grooming up the hierarchy (TauKr)	[2]True	[2]NS	0.34***	0.04
Grooming up the hierarchy High > Low	[2]True		U=100***	
11) Grooming partners of similar rank (TauKr)	[2]True	[2]NS	0.13**	-0.01
Grooming partner of similar rank High > Low	[2]True		U=100***	
12) Reconciliation with valuable partners (TauKr)	[2]True	[2]True	0.37***	0.11**
Reconciliation valuable partners High > Low	[2]NA		U=78*	
Coalition patterns				
Intensity of Aggression	Despotic and Egalitarian combined[4]		High	Low
13) % of fights involving coalitions	[5]5% / 9%		10%	7%
14) % of triadic coalitions (3 individuals)	[6]75%		96%	98%
15) % of tetradic coalitions (4 individuals)	[6]25%		4%	2%

Table 3. cont.

Intensity of Aggression	Despotic and Egalitarian combined[4]		High	Low
Coalition types against adults				
16) Conservative coalitions %	[7]70%		71%	29%
17) Bridging coalitions %	[7]26%		21%	27%
18) Revolutionary coalitions %	[7]4%		8%	44%
Jonckheere-Terpstra test (C>B>R)			JT=0***	JT=205 NS
Patterns related to triadic awareness				
19) Recipient < Target < Supporter[8]	[8]84%		+(67%)***[15]	-(24%)***[15]
20) Support given to 'friend'[9]	[9]67%		+(70%)***[15]	+(54%)*[15]
21) Support given to 'friend'[10]	[10]NA		+(69%)***[15]	+(53)%* [15]
TauKr correlations				
22) Reciprocation of support (TauKr)	[11]True		0.38***	0.27***
23) Grooming for Support Received (TauKr)	[12]True		0.36***	0.29***
24) Support for Grooming Received (TauKr)	[13]True		0.29***	0.36***
25) Reciprocation of opposition (TauKr)	[14]NS	NA	-0.11**	0.29***

Table 3. **Dominance, affiliation and coalition patterns among females: empirical data and GrooFiWorld.** Coalition patterns: empirical results of egalitarian and despotic species are lumped except for the frequency of coalition types which are reported in a single study (Vasey 1996: 10 in Table 1). Results represent the average over 10 runs. P-value based on the Bonferroni correction: *=p<0.05; **=p<0.01, ***=p<0.001. [1]Among all individuals. [2]See our previously analyzed empirical data in: (Puga-Gonzalez et al. 2009); [3](Hemelrijk et al. 2008a). [4] These species include more than macaques, also baboons and chimpanzees. [5]Excluding vocal coalitions/including vocal coalitions. [6](calculated from: de Waal & Harcourt 1992). [7](Vasey 1996). [8](Schino et al. 2006): This study concerns males and females combined; [9](Perry et al. 2004); [10]Omitting support from the relationship quality index (Perry et al. 2004); [11]8,19,21,22 in Table 1; [12]3,4,8,9,11,13,22 in Table 1; [13]6,7,8,22 in Table 1.[14](Hemelrijk & Ek 1991) . [15]Supporter higher ranking than target and recipient: + more frequent than chance; - less frequent than chance.

resembling results for female chimpanzees (Hemelrijk & Ek 1991), and it is even unidirectional (25 in Table 3). In addition to empirically-derived hypotheses, we also studied other correlations of opposition with grooming and support. At both intensities of aggression in the model, females oppose those individuals more frequently whom they support more often (11 in Table 2 in appendix) and by whom

they are groomed more often (10 in Table 2 in appendix) and females receive opposition more often from those partners whom they groom and support more frequently (9, 12 in table 2 in appendix). It thus appears that 'services' are exchanged for harmful acts.

There are several significant differences at a *high versus low intensity* of aggression: 1. The percentage of coalitions that is conservative is higher (high vs low intensity of aggression, Mann-Whitney $U=100$, $p<0.001$) and the percentage that is revolutionary is lower (high vs low intensity of aggression, Mann-Whitney $U=100$, $p<0.001$), 2. Individuals more frequently show 'triadic awareness of choice of coalition partners at high than at low intensity, 3. The degree of reciprocity of support is greater (1 in Table 3 in appendix), 4. The correlation for exchange of grooming for support is stronger and the correlation for support for grooming is weaker (20, 21 in Table 4; 2, 3 in Table 3 in appendix), 5. Opposition is unidirectional at high intensity and bidirectional at low intensity of aggression (4 in table 3 in appendix).

Causation of coalition patterns in the model and predictions for empirical data

In empirical studies, patterns of reciprocation and exchange are considered to be based on record-keeping, so-called 'calculated reciprocity', if they remain statistically significant when proximity, rank, kinship and age are partialled out (de Waal & Luttrell 1988; Hemelrijk & Ek 1991; Gomes & Boesch 2009), as in this case they are not considered to be a side-effect of these factors (de Waal & Luttrell 1988; de Waal & Brosnan 2006). Unexpectedly, all the correlations for reciprocation and exchange in the model remain significant even when proximity and rank are partialled out (age and kinship are absent in the model, Tables 3 in appendix). Thus, correlations in the model resemble empirical data. However, in the model, no records are kept by the individuals on acts given and received, nor on support or on grooming.

Because partial correlations may not sufficiently exclude the dynamics of rank and proximity (Hemelrijk 1996a), we did experiments in the model in which we removed the effects of rank and of proximity more rigorously than is achieved

Model-based hypotheses for adult females:	Empirical data
A) In general:	
1) Revolutionary coalitions are more frequent the higher the percentage of males in the group	NA
2) In larger groups the conciliatory tendency is higher and the correlation for the valuable relationship hypothesis is stronger.	NA
3) The stronger the degree of social facilitation, the higher the frequency of support and the percentage of polyadic support	NA
4) The number of coalitions among females is higher the higher their percentage in the group	NA
Females:	
5) Groom those more often that they support more frequently	Pro: (Hemelrijk & Ek 1991)
6) Receive grooming more frequently from those that they more often receive support from	NA
7) Receive aggression more often from those that they more frequently receive opposition from	NA
8) Aggress those more often that they oppose more frequently	NA
9) Groom those more often that they more frequently receive opposition from	Contra: (Hemelrijk & Ek 1991)
10) Oppose those more often that they more frequently receive grooming from	NA
11) Oppose those more often that they more frequently support	NA
12) Support those more often that they more frequently receive opposition from	NA
B) In egalitarian species:	
13) Opposition is bidirectional	Contra:(de Waal & Luttrell 1988)
C) In despotic species:	
14) Females receive support more frequently from partners, the higher the rank of their partner	Pro: (Hemelrijk & Ek 1991)
15) Opposition is unidirectional	Pro: (de Waal & Luttrell 1988)
16) Supporters are significantly more often higher ranking than the target of the coalition, even if the recipient of support ranks below the target	Pro: (Range & Nöe 2005; Schino et al. 2006)
D) In despotic compared to egalitarian species[1]	
17) Coalitions are less often revolutionary	NA[1]
18) Females will more often solicit others that are higher in rank than both the solicitor and target.	NA
the correlation at a group level for:	
19) reciprocation of support is stronger	NA
20) the exchange of grooming for support is stronger	NA
21) the exchange of support for grooming is weaker	NA

Table 4. Model-based hypotheses.

[1]This is in line with the model-based predictions by van Schaik and co-authors (van Schaik et al. 2004)

by partial correlation. We removed the effects of three different assumptions in turn, i.e., that interactions are influenced by social facilitation and by proximity (by making individuals choose interaction partners at random) and that there are differences among individuals in dominance rank (by shuffling ranks between adults). We investigated the consequences for the following eight patterns: percentage of coalitions, relative frequency of three coalition types, two patterns related to triadic awareness, and the occurrence of significance in four correlations (combined over 10 replica-runs), i.e., of reciprocation of support and opposition, grooming for receipt of support, and support for the receipt of grooming. The greatest reduction (i.e., 94%) in the number of significant patterns occurred when simultaneously disabling the effects of both proximity and rank, a slightly lower reduction occurred when merely disabling the effects of proximity, i.e., 50% at both intensities, a still lower reduction when omitting social facilitation (i.e., 50% at high intensity and 25% at low intensity) and when shuffling ranks, i.e., 38% at high intensity and 12% at low intensity (13-22 in Table 5).

This led to the following explanations for the coalition patterns:

The *percentage of fights* that involved coalitions are a consequence of social facilitation and proximity, as can be seen from their decrease without these assumptions (13 in Table 5). Social facilitation strengthens the effects of proximity by increasing the likelihood of forming coalitions, because individuals that are close to a fight are activated next.

The *type of support* is a side-effect of risk aversion and individual differences in dominance rank, as can be seen when ranks are shuffled. In this case, the three types of support become similar in their frequency (14-16 in Table 5).

With reference to *triadic awareness* in the choice of coalition partners, the supporter is higher in rank than both the target and the receiver, as is the case for empirical data. However, in the model this is only found at high intensity of aggression and not at a low intensity (19 in Table 3). This pattern arises as a side-effect of rank and proximity, because it disappears if the effects of rank and space are removed (17B, 17C in Table 5). Clearly, individuals that are closer will have more opportunities to support each other and, at a high intensity, individuals that

Table 5

	A. No social facilitation		B. Ranks shuffled		C. Random interaction partners		D. Random interaction partners and ranks shuffled		E. Complete Model	
Intensity of Aggression	High	Low	High	Low	High	Low	High	Low	High	Low
Dominance Style										
1) Gradient of the hierarchy (CV)[1]	0.75	0.36	0.71	0.38	0.70	0.36	0.71	0.38	0.72	0.36
2) Unidirectionality of aggression (TauKr)	-0.19**	0.48***	**0.46*****	0.53***	-0.54***	**-0.05**	**0.00**	**0.01**	-0.13**	0.51***
3) Time spent fighting (%)	14	20	16	20	NA	NA	NA	NA	13	17
4) Relative female dominance	0.29	0.00	**0.50**	**0.50**	0.16	0.00	0.50	**0.50**	0.22	0.00
5) Mean distance among all group members	26	22	**23**	**25**	NA	NA	NA	NA	29	25
6) Centrality of dominants (Tau)	-0.44***	-0.09	**0.06**	**-0.03**	NA	NA	NA	NA	-0.40**	-0.10
Affiliative patterns										
7) Time spent grooming (%)	18	22	**23**	**19**	NA	NA	NA	NA	17	20
8) Conciliatory Tendency	19	28	**32**	32	**0**	**0**	**0**	**0**	21	31
9) Grooming reciprocation (TauKr)	0.36***	0.51***	0.58***	0.55***	**-0.37*****	[2]**-0.01****	**-0.03**	**-0.02**	0.39***	0.54***
10) Grooming up the hierarchy (TauKr)	0.34***	[2]**0.05***	**0.00**	0.00	0.50***	**0.14****	0.09**	**0.09****	0.34***	0.04
11) Grooming partners of similar ranks (TauKr)	0.17***	0.01	**0.00**	-0.03	0.07**	0.02	**-0.01**	-0.01	0.13**	-0.01
12) Reconciliation with valuable partners	0.36***	0.13**	0.15***	0.14**	**0.00**	**-0.02**	**-0.03**	**-0.03**	0.37***	0.11**
Coalitions patterns										
13) % of fights involving coalitions	**3 %**	**3 %**	9	9	**2 %**	**1 %**	**2**	**2**	10%	7%
14) Conservative coalitions %	52 %	27 %	**34 %**	**32 %**	64 %	28 %	**36 %**	**34 %**	71%	29%
15) Bridging coalitions %	37 %	27 %	**33 %**	**34 %**	23 %	25 %	**29 %**	**32 %**	21%	27%
16) Revolutionary coalitions %	11 %	46 %	**33 %**	**34 %**	13 %	47 %	**35 %**	**34 %**	8%	44%
Jonckheere-Terpstra test (C>B>R)	JT=0***	JT=240 NS	JT=127 NS	JT=167 NS	JT=6***	JT=220 NS	JT=147 NS	JT=155 NS	JT=0***	JT=205 NS

Table 5 cont.

	A. No social facilitation		B. Ranks shuffled		C. Random interaction partners		D. Random interaction partners and ranks shuffled		E. Complete Model	
Intensity of Aggression	High	Low	High	Low	High	Low	High	Low	High	Low
17) Recipient < Target < Supporter (%)[3]	+(74)***	-(25)***	**-(34)*****	-(35)***	**+(62) NS**	-(23)***	**-(34)*****	-(35)***	+(67)***	-(24)***
18) Support given to 'friend' (%)[3]	+(56)*	**+(54) NS**	**+(51) NS**	**+(54) NS**	+(77)***	+(54)*	**+(53) NS**	**+(57) NS**	+(70)***	+(54)*
TauKr correlations										
19) Support Reciprocation (TauKr)	**[2]0.05***	**0.08****	0.21***	0.27***	**[2]0.02***	**0.04**	**0.00**	**0.01**	0.38***	0.27***
20) Grooming for Support Received (TauKr)	**0.23*****	**0.18*****	**0.26*****	0.32***	**0.11****	**-0.01**	**0.02**	**0.01**	0.36***	0.29***
21) Support for Grooming Received (TauKr)	**0.18****	**0.23*****	**0.33*****	0.39***	**-0.01**	**-0.02**	**0.02**	**0.02**	0.29***	0.36***
22) Opposition given and opposition received	**0.00**	0.14**	**0.20*****	0.29***	-0.07*	0.01*	**0.01**	**-0,03****	-0.11**	0.29***

Table 5. Dominance, affiliation and coalition patterns among females in the model when taking out different assumptions.
Results represent the average over 10 runs. P-value based on the Bonferroni correction: *=p<0.05; **=p<0.01, ***=p<0.001. In **bold:** results that differ from the full model. NA=Not Available. [1] Among all individuals. [2]4 correlations (5% of 72 correlations) are considered to be a type I error. [3]Supporter higher ranking than target and recipient: + more frequent than chance; - less frequent than chance

are of higher rank than an opponent and receiver will experience less risk in providing support. Since there are no data on triadic awareness among female primates in egalitarian species, we predict that in empirical studies on egalitarian species, females will also solicit others that are higher in rank less often than both the solicitor and target, than is the case in despotic species (18 in Table 4).

Reciprocation of support among females is due to social facilitation and proximity. This is clear, because it is weakened when social facilitation is disabled and it disappears after taking out proximity and making individuals randomly choose interaction partners (19AC in Table 5). Reciprocation of support emerges because certain individuals are more often in close proximity than other individuals and, thus have more opportunities for attacking the same opponents. In fact, two individuals may attack the same target in turn for several consecutive activations when the victim, by fleeing from one opponent, ends up in the space occupied by the other opponent, a kind of spatial entrapment (Hemelrijk 1997, VideoS1). Such immediate reciprocation happens at high intensity in 25% of the cases of support and at low intensity in 7% of cases. When we exclude immediate reciprocation, the patterns in Table 3 remain, but the percentage of fights involving coalitions decreases at high intensity of aggression (from 10 to 7%, 1 in Table 4 in appendix), and reciprocation of support is weakened at both intensities, but still significant in all runs (5 in Table 4 in appendix). Further, the interchange of grooming for receipt of support and of support for receipt of grooming remains similar in significance without immediate reciprocation (6,7 in Table 4 in appendix). This interchange emerges as a side-effect of proximity and rank: these correlations are significantly weakened when the effects of social facilitation and proximity are excluded and become non-significant if females choose their interaction partners at random and their ranks are simultaneously shuffled (20, 21 in Table 5).

Opposition in the model is bidirectional at low intensity of aggression (thus, individuals more often oppose those partners from whom they receive more opposition (Hemelrijk 1990a)) and unidirectional at high intensity of aggression (25 in Table 3). This also applies if we exclude immediate reciprocation (8 in Table 4 in appendix). This is expected, as no separate rule for support (or opposition) has

been added (both are in the eye of the observer), opposition *is* a specific instance of dyadic aggression, and dyadic aggression is more bidirectional at low than at high intensity of aggression (2 in Table 3) (Hemelrijk 1999a; Hemelrijk 2000a; Puga-Gonzalez et al. 2009). Furthermore, as expected, opposition is significantly correlated with the remaining cases of dyadic aggression (6, 7 in Table 2 in appendix). Patterns of bidirectionality at low intensity of aggression and unidirectionality at high intensity disappear after taking out both spatial structure and the effects of ranks by shuffling ranks (22D in Table 5).

Correlations for reciprocation of opposition and for opposition with grooming and support remain when immediate reciprocation is excluded, Table 4 in appendix. They are a side-effect of correlations for dyadic aggression with grooming and support (8-12 in Table 2 in appendix). The patterns of bi- and unidirectionality of opposition, correlations for opposition with aggression and for 'exchange' between opposition and support or grooming may be used directly as model-based predictions to be tested empirically (7-12, 13, 15 in Table 4).

Differences between high and low intensity

Regarding patterns indicating triadic awareness in the choice of coalition partner, supporters are more often higher ranked than the target and the receivers at high intensity compared to low intensity, because due to the steep hierarchy, supporters of lower rank experience more risk of being defeated, whereas such risks for individuals of different ranks are more similar at low intensity due to the weak hierarchy.

With reference to the *type of coalitions among females*, the percentage of conservative coalitions is higher at high aggression intensity, as a consequence of the hierarchy being steeper than at low intensity (1 in Table 3). The steeper hierarchy increases the aversion of attacking higher ranking individuals and the likelihood of attacking lower ranking individuals, thus leading to conservative coalitions most often, and to bridging coalitions at an intermediate frequency (16-18 Table 3). In contrast, revolutionary coalitions between females are more frequent at low intensity of aggression. This is due to the weaker hierarchy and the

stronger subordinance of females to males at a low aggression intensity than at a high aggression intensity (4 in Table 3), which resembles the greater subordinance of female egalitarian macaques to males compared to despotic macaques (Hemelrijk et al. 2008a). Indeed, when we exclude coalitions of females against males at a low intensity, revolutionary coalitions become less frequent than bridging and conservative coalitions, as is the case for high intensity, C>B>R (Jonckheere-Terpstra test, n=10, JT = 28.5, $p<0.001$). At low intensity, the number of opportunities for females to attack higher ranking individuals is greater than at high intensity for two reasons: 1) the subordinance of females relative to males is greater than at high intensity (4 in Table 3) and 2) the percentage of males in the group is higher (30% vs. 20% at high intensity). With reference to the percentage of males, if the percentage of males in the group is increased from approximately 25% (20% at high intensity or 30% at low intensity), via 50% to 70 % in the model, the number of revolutionary coalitions among females increases from 8 to 10 to 20% at high intensity and from 44 to 55 to 73 % at low intensity. Thus, we predict that the higher the percentage of males in the group, the higher the frequency of revolutionary coalitions compared to conservative or bridging coalitions (1 in Table 4). Because empirical data on coalition types in egalitarian species are lacking, this result serves as a prediction: coalitions among females in egalitarian species should more often be revolutionary than in despotic species (17 in table 4).

At a high intensity, females *reciprocate support* more often than at a low intensity, because reciprocation more often happens immediately. This is because individuals in the group are spaced further apart (5 in Table 3) and series of immediate reciprocation thus continue for longer because there is less 'interference' from other individuals close by. The greater spacing of individuals in the group is a consequence of the repeated fleeing of lower ranking individuals, due to the steeper hierarchy (Hemelrijk 1999a). Because the spacing of individuals in groups of despotic macaques is also greater than that in egalitarian macaques, we predict that empirical data for despotic societies compared to egalitarian societies will reveal relatively less frequent revolutionary support and conservative support to be more frequent, and support to be reciprocated more often (17,19 in

Table 4). Furthermore, there is a stronger correlation for exchange of grooming for support and a weaker correlation for support for grooming at a high intensity than at a low intensity (20, 21 in Table 4; 2, 3 in Table 3 in appendix). This is a consequence of the fact that at high intensity, both variables, grooming and receipt of support, are significantly positively correlated with the rank of the partner (10 in Table 3; 3 in Table 2 in appendix), while this is not the case for the variables of support and receipt of grooming (4, 5 in Table 2 in appendix). This results in the model-based prediction for high intensity, that individuals receive support more frequently from partners, the higher the rank of the partners, for which there is also some empirical evidence (14 in Table 4). Other patterns, such as the association between grooming other individuals and supporting them (1,2 in table 2 in appendix), can also be used as hypotheses for empirical data (5,6 in Table 4).

Sensitivity-analysis of coalition patterns

The patterns of reciprocation and exchange appear to be robust against changes to the parameters, as they depend only weakly on the percentage of coalitions, the number of individuals and the degree of aversion of risks. They remain significant as long as the percentage of coalitions is above ~4% for females (see caption in Table 5 in appendix) and the number of females is at least 8 at high and 12 at low intensity of aggression (Table 5 in appendix). If the risk aversion is increased from winning twice mentally before attacking to winning mentally 3, 4 or 5 times, the patterns of types of support, exchange and reciprocation of support and opposition remain qualitatively the same (Table 5 in appendix).

The patterns of reciprocation of support and its exchange for grooming also appear to be robust against changes in the behavioural rules. They appear to remain significant under the following experimental manipulations (see appendix table 1): 1) when we change the order of the rules for aggression and grooming (by reversing the order, by first considering grooming and then fighting and by taking a random order in which to consider both acts, column AB in appendix table 1), 2) when we omit the induction of grooming by anxiety and instead make individuals always groom when they expect to lose a fight (C in appendix table 1), and 3) when

omitting the aversion of the risk of losing a fight, but giving individuals a specific chance of attacking at high intensity and at low intensity (see experimental setup), independent of the risks involved (column D in appendix table 1). The proportions of different types of coalitions only changed compared to the full model when risk-aversion at high intensity was omitted (Appendix table 1). Note that the manipulation of omitting risk aversion is similar to shuffling ranks. With reference to reciprocation (bidirectionality) of opposition, unidirectional opposition at high intensity depends on risk aversion and on the order of the behavioural rules in the same way as dyadic aggression (22 in columns A and D in Appendix table 1). Patterns that may be considered indications of triadic awareness in the choice of coalition partners depend on risk aversion and on the order of the behavioural rules at high aggression intensity (17, 18 in Appendix table 1).

Discussion

We have shown that our model does a good job at predicting the relative percentage of different types of coalitions, patterns indicative of triadic awareness in the choice of coalition partners and patterns of reciprocation and exchange. The model succeeds at this by reducing the problem to the right variables. It reveals how patterns of support and opposition, their reciprocation and exchange may emerge as a side-effect of socio-spatial structure through self-organization. The processes of socio-spatial structuring are mostly a consequence of dominance interactions (Hemelrijk 1999a; Hemelrijk 2000a). Rank-related patterns (such as more frequent grooming of other individuals higher in rank at high intensity of aggression) are due to rank and aversion of the risks of being defeated (Puga-Gonzalez et al. 2009). Patterns of support are due to socio-spatial structure, with social facilitation playing a lesser role. These patterns arise because the socio-spatial structure implies that certain individuals are often close to specific other individuals. This automatically causes the occurrence of support (and opposition) in fights, reciprocation and exchange for grooming. The experiments in the model and the sensitivity analysis of its parameters and behavioural rules show that the occurrence of support, its reciprocation and exchange are robust. This is surprising,

because the model drops 'rational' or 'deliberate' choices by individuals to support others in fights, it lacks triadic awareness and lacks record-keeping. Similar processes of socio-spatial structuring through dominance interactions and differences in fighting power (rank) and avoidance of risks, may also automatically induce patterns of support and opposition, their reciprocation and exchange in real primates. Indeed spatial centrality of dominants is also found in real primates (Itani 1954; Imanishi 1960; Yamada 1966; Kaufmann 1967; Robinson 1981; Wada & Matsuzawa 1986; Lopez-Lujan et al. 1989; Janson 1990; Rasmussen & Farrington 1994) and seems stronger in despotic species than in egalitarian species (Hemelrijk 1999a).

It is worth comparing existing explanations of a number of empirical findings to those of the present model.

First, the finding that chimpanzees reciprocated both support and opposition and that macaques reciprocated only support but not opposition has been taken as evidence that the chimpanzees simultaneously consider more aspects of social relationships than macaques and that chimpanzees are revengeful, but macaques are not (de Waal & Luttrell 1988; but see Jensen et al. 2007). However, no reciprocation of opposition was found for chimpanzees in the same data set when data were analyzed on an annual basis (instead of being lumped over five consecutive summers), neither was opposition reciprocated when studied by sex (Hemelrijk & Ek 1991). Absence of reciprocation of opposition is in line with the model because reciprocation of opposition is absent at high intensity and we assume that chimpanzees in this colony are despotic rather than egalitarian, because the dominance style of chimpanzees is most despotic in communities (such as Taï) where grouping is densest (Wittig & Boesch 2003). In this captive colony, grouping is dense and frequency of aggression is high as well, which results in a more despotic dominance style than when the individuals in groups are more spaced apart and aggression is rarer, as is the case in natural conditions (Hemelrijk 2011). Despotism in this captive colony is also apparent because the higher the rank of the partner, the more often the females in this colony groom others (Hemelrijk & Ek 1991), which is a pattern that is typical of macaques that are

despotic, but not of those that are egalitarian (Butovskaya 2004).Thus, lack of reciprocation of opposition in the Arnhem colony is in line with the model, which suggests that reciprocation of opposition is constrained by avoidance of the risks of attacking higher ranking individuals because the hierarchy is steep. In contrast, if the hierarchy is weak, opposition automatically becomes more reciprocal (also referred to as bi-directional), because the mutual risks are more similar. Thus, the model offers up the difference in the hierarchical gradient as an alternative explanation to the usually assumed difference in intelligence.

Second, Silk (1992) finds reciprocation of support and opposition in male bonnet macaques (*Macaca radiata*). This is also in line with the model as bonnet macaques are egalitarian (Thierry 2004). Silk reasons that if individuals classify other individuals into allies and adversaries, they should more often give support to those whom they oppose less. Contrary to this, her data show instead that individuals more frequently support those individuals that they oppose more often. This association reflects what our model predicts.

Third, stronger patterns of coalition formation have been found in despotic than egalitarian species among female macaques and this has been attributed to the stronger effects of kin and nepotism (Thierry 1990). Although this may be true, our model indicates possible alternative causes. It suggests that stronger reciprocation of support among despotic females than among egalitarian females is due to the higher degree of immediate reciprocation, which is caused by the greater spacing between females in the despotic group. The lower spatial density in the model lengthens the chains of mutual support in fights that are undisturbed (Hemelrijk 1996a).

Fourth, empirical data reveal that individuals solicit support by headflagging more often to other individuals ranked above them and to those with better relationships with themselves than with the opponent (Silk 1999; Perry et al. 2004; Range & Nöe 2005; Schino et al. 2006). In the model, although headflagging is absent, individuals still receive more support from higher ranking individuals, but this is not due to triadic awareness in the model. Instead, it arises as a side-effect of rank and proximity (17 in Table 5). Individuals may also be more easily solicited in

reality when they are closer to the solicitor and the fight. Those individuals that are closer to the solicitor are the individuals that experience less risk, thus, they will be the individuals that are higher ranked than the other two (i.e., the potential receiver and the target).

Fifth, in several species, individuals more often support those individuals in fights that they also groom more frequently (Hemelrijk & Ek 1991; Watts 2002). This has been explained by cognitive mechanisms, but classical conditioning has also been suggested (Hemelrijk & Ek 1991; Berghaenel et al. 2010). The present model provides an even simpler explanation, the association is a side-effect of spatial proximity.

Sixth, when patterns of reciprocation and exchange remain significant, after partialling out proximity, kinship, rank and age, it is concluded that reciprocation and exchange are 'calculated' by record-keeping (de Waal & Luttrell 1988; Hemelrijk & Ek 1991; Gomes & Boesch 2009). However, these are not calculated in the model and patterns of reciprocation and exchange still remain after partialling out rank and proximity. Apparently, these statistical procedures do not deal satisfactorily with complex nonlinear effects due to the socio-spatial structuring (Hemelrijk 1996a; Hemelrijk 1996b; Hemelrijk 2000a), because when we remove the effects of proximity (or both rank and proximity) by an experimental procedure in the model, reciprocation and exchange are no longer significant (19-22CD in Table 5). Thus, the model shows that it does not suffice to partial out proximity in order to eliminate its effects. It appears that the partial correlation has not completely excluded the dynamics of these effects because a partial correlation represents a linear, additive approach and effects of fights on spatial structure are nonlinear (Sumpter 2006). This serves as an important warning for the interpretation of these correlations.

Two important features of our work, its parsimony and falsifiability, are reached by integrating many aspects, such as spatial position, fights and grooming. As a consequence, the model produces explanations that are cognitively parsimonious and hypotheses that are easily tested because they concern aspects on which much empirical data are available, such as dominance style (Hemelrijk

1999a; Hemelrijk 2005; Hemelrijk et al. 2008a), affiliative behaviour (Puga-Gonzalez et al. 2009) and coalitions in egalitarian and despotic societies (Table 4).

Due to the repeated process of validation of our model over a decade, we have gained more and more confidence in it (Sornette et al. 2007); first, we have shown that the patterns of the model at low and high intensity of aggression resemble, respectively, egalitarian and despotic societies regarding dominance style (namely, frequency of aggression, average distance between individuals, symmetry of aggression, spatial centrality of dominants, and decrease of aggression when becoming 'familiarized') (Hemelrijk 1999a; Hemelrijk 2000a; Hemelrijk & Gygax 2004); second, we have predicted and confirmed greater female dominance relative to males when dominance style is steeper and when the percentage of males in the group is higher (Hemelrijk et al. 2008a); third, we have shown that adding a rule of intending to groom to avoid the risks of losing a fight and when being anxious led to patterns of grooming and reconciliation resembling empirical data for both dominance styles in macaques (Puga-Gonzalez et al. 2009); fourth, in the present paper, we show that the model also reveals patterns of support (and opposition), reciprocation and interchange for grooming that resemble those in real primates.

A point of critique by de Vries on an earlier study of our model (de Vries 2009) has been that the directional inconsistency of the dominance interactions is too low compared to that found in empirical data. Due to the increased risk aversion in the current model (but for the same number of fights), directional inconsistency has become higher (0.91 among adults at a high intensity), while qualitatively maintaining all reported results (Table 5 in appendix) (Hemelrijk 1999a). This value resembles that found in empirical data on despotic macaques, *M. fuscata* and *M. fascicularis* (Table 2 of de Vries). Whether the directional inconsistency characterizes dominance style in a useful way is, however, doubtful, because de Vries shows it to be higher in egalitarian macaques than in despotic macaques (de Vries 2009), whereas we would expect the opposite to hold.

In the present study, the frequency of polyadic fights is lower than in reality. Note that the model presented here was constructed before looking at data on

coalitions. Instead, it was loosely tuned to grouping and aspects of dominance style and percentage of grooming (Puga-Gonzalez et al. 2009). The frequency of polyadic coalitions may be heightened by increasing the biological realism of the model, e.g., by including sexual behaviour. When we add sexual attraction of males to females and make females come into oestrus asynchronously, males have been shown to cluster close to a female in oestrus (Hemelrijk et al. 2003). Therefore, we may expect a higher number of polyadic coalitions among these males (Schuelke et al. 2010).

The model is an extreme simplification of reality. Its social complexity and biological realism could be increased, e.g., by including recruitment behaviour, social bonding, feeding behaviour, kin-relations, different sex-age classes, immigration or emigration or sexual behaviour. It should be stressed that our model is not meant to show that primates are unintelligent. That primates are intelligent is proven, for instance by the fact that they show intentional imitation (Buttelmann et al. 2007) and intentional exchanges in experimental settings (Dufour et al. 2009). For some species, the model may represent coalitions as they are at present, but for others they may represent coalitionary behaviour as it was early in evolution, because coalitions of these species have recently become cognitively more sophisticated. In future, we will also use models to study more sophisticated cognitive strategies of supporting others in fights. However, it should be noted that even if primates are using more intelligent strategies for coalitions, there will still be an effect of socio-spatial structure on coalition patterns (see chapter 7 for results of implementation of coalition rules in the GrooFiWorld model).

With regard to evolutionary explanations, our model indicates that selection operates on complexes of interconnected traits rather than single traits alone. For instance, according to our model, the evolution of a higher intensity of aggression versus a milder intensity is associated with automatic consequences for many traits, e.g., a steeper hierarchy, greater female dominance over males, less reconciliation, fewer revolutionary coalitions, stronger reciprocation and exchange of support. Therefore, theories will need to explain the evolution of the whole

complex of integrated traits. To relate the evolution of this complex to ecological conditions, models must examine its evolution for several distributions of food in a similar way as has been done in models related to culture (van der Post & Hogeweg 2008; van der Post et al. 2009).

Our results have three clear implications. First, in contrast to the common belief in empirical studies (de Waal & Luttrell 1988; Hemelrijk & Ek 1991; Gomes & Boesch 2009), correlations for reciprocity and exchange in the model remain significant after partialling out proximity and rank, even though these correlations are not due to intentional or internally-guided rules for reciprocation or exchange. A different method other than partial correlation is apparently required to exclude the effects of proximity and of rank in the causation of patterns of reciprocation and exchange. Secondly, for scientists interested in the actual cognitive deliberation underlying spontaneous social behaviour in groups of primates, it is essential to study the spatial positioning of individuals in relation to their social behaviour. This is necessary in order to see to what extent the social behaviour can be attributed to socio-spatial structuring and what patterns are left that must be attributed to active deliberation. Thirdly, this model presents a starting point for developing a theory of social behaviour that arises among individuals if only simple cognition is present. Such theories are badly needed (Hemelrijk 2011; van der Vaart et al. In press).

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We would like to thank the Self-organisation Lab for discussion**.**

Appendix

Here I present the extra results that have been mentioned and discussed in the chapter 3.

Results

Extra results concern the following: A sensitivity analysis of the complete model regarding its behavioural rules, such as the order and assumptions regarding anxiety and risk aversion (Table 1), associations at a group level among grooming, support, opposition and rank (Table 2 in appendix), correlations for reciprocation and exchange of support partialling out rank and proximity (Table 3 in appendix), coalition patterns after controlling for immediate reciprocity (Table 4 in appendix), and sensitivity analysis of parameters of the complete model (group size, sex ratio and degree of risk aversion) (Table 5 in appendix) .

Sensitivity analysis of the behavioural rules of the individuals:

We studied the consequences of the following manipulations of behavioural rules: a) aggression and grooming in the reversed order of that of the complete model. In this case, individuals considered first whether or not to groom the other and subsequently whether or not to attack, b) considering grooming and aggression in a random order. Here individuals had a random chance of 50% of first considering to groom or to attack, c) actively always grooming others upon estimating to lose a fight, thus, individuals did not take into account their anxiety level like they did in the complete model, d) considering attacking another by chance (namely 15%, the same percentage as in the complete model), thus, not depending on the chance to win as individuals did in the complete model.

Table 1

Behavioural Rules	**A)** First considering grooming; then, fighting		**B)** Random order of considering grooming and fighting		**C)** No anxiety-induced grooming		**D)** No Risk Aversion		**E)** GrooFiWorld Complete Model	
Intensity of Aggression	High	Low	High	Low	High	Low	High	Low	High	Low
Dominance Style										
1) Gradient of the hierarchy (CV)[1]	**0.54**	0.36	0.62	0.37	0.69	0.38	0.71	0.36	0.72	0.36
2) Unidirectionality of aggression (TauKr)	**0.03**	0.32***	**0.09****	0.49***	-0.11*	0.52***	**0.45*****	0.50***	-0.13**	0.51***
3) Time spent fighting (%)	**5**	**6**	7	10	12	16	13	17	13 %	17 %
4) Relative female dominance	0.11	0.00	0.15	0.0	0.23	0.00	0.21	0.00	0.22	0.00
5) Mean distance among all group members	23	23	30	26	27	25	**24**	**26**	29	25
6) Centrality of dominants (Tau)	**-0.07**	**0.02**	-0.29*	-0.12	-0.36**	-0.04	-0.26**	-0.03	-0.40**	-0.10
Affiliative patterns										
7) Time spent grooming (%)	**37**	**38**	20	23	19	21	**27**	20	17	20
9) Grooming reciprocation (TauKr)	0.67***	0.67***	0.71***	0.71***	0.40***	0.55***	0.62***	0.60***	0.39***	0.54***
10) Grooming up the hierarchy (TauKr)	**0.00**	0.00	**0.00**	0.02	0.32***	0.03	**0.00**	0.02	0.34***	0.04
11) Grooming partners of similar ranks (TauKr)	**0.01**	0.00	**0.02**	0.02	0.12**	0.02	**-0.01**	0.00	0.13**	-0.01

Table 1 cont.

Behavioural Rules	**A)** First considering grooming; then, fighting		**B)** Random order of considering grooming and fighting		**C)** No anxiety-induced grooming		**D)** No Risk Aversion		**E)** GrooFiWorld Complete Model	
Intensity of Aggression	High	Low	High	Low	High	Low	High	Low	High	Low
Coalitions patterns										
13) % of fights involving coalitions	**2**	**3**	**4**	**4**	10	7	**6**	7	10	7
14) Conservative coalitions %	57	27	66	29	74	28	**31**	23	71	29
15) Bridging coalitions %	26	24	21	25	18	27	**31**	23	21	27
16) Revolutionary coalitions %	17	49	13	46	8	45	**38**	54	8	44
Patterns related to triadic awareness										
17) Recipient < Target < Supporter (%)[1]	**-(49)NS**	-(23)***	**+(55)NS**	-(24)***	+(64)***	-(24)%***	**-(28)*****	-(17)***	+(67)***	-(24)***
18) Support given to 'friend' (%)[1]	**+(52)NS**	**+(52)NS**	**+(58)NS**	**+(53)NS**	+(72)***	+(53)%*	**+(53)NS**	+(55)*	(+70)***	+(54)*
TauKr correlations										
19) Support Reciprocation (TauKr)	0.15*	0.08**	0.17**	0.13**	0.41***	0.27***	0.16**	0.17**	0.38***	0.27***
20) Grooming for Support Received (TauKr)	0.10**	0.13**	0.14**	0.19***	0.36***	0.28***	0.22***	0.25***	0.36***	0.29***
21) Support for Grooming Received (TauKr)	0.13**	0.16**	0.18**	0.23***	0.30***	0.35***	0.27***	0.33***	0.29***	0.36***
22) Opposition given and opposition received	**0.01**	**0.00**	-0.03*	0.11**	-0.07**	0.25***	**0.12****	0.20***	-0.11**	0.29***

Table 1. Sensitivity analysis of the behavioural rules. Patterns among females. Results represent the average over 10 runs; P-value based on the Bonferroni correction: *p=<0.05; **p=<0.01, ***p=<0.001. In **bold:** results that differ from the full model. [1]Supporter higher ranking than target and recipient: + more frequent than chance; - less frequent than chance.

Intensity of Aggression	High	Low
1) Grooming and Support	0.25***	0.35***
2) Receipt of grooming and receipt of support	0.19**	0.28***
3) Receipt of support and rank of partner	0.26***	0.14
4) Receipt of grooming and rank of partner	[1]-0.05*	-0.02
5) Support and rank of partner	0.06*	0.00
6) Aggression and opposition	0.52***	0.43***
7) Receipt of aggression and receipt of opposition	0.47***	0.33***
8a) Opposition and Opposition Received	-0.11**	0.29***
8b) Aggression and aggression received	-0.11**	0.48***
9a) Grooming and Opposition Received	0.43***	0.35***
9b) Grooming and aggression received	0.63***	0.53***
10a) Opposition and Grooming Received	0.31***	0.41***
10b) Aggression and grooming received	0.46***	0.53***
11a) Support and Opposition	0.13**	0.28***
11b) Support and aggression	0.20***	0.37***
12a) Support and Opposition Received	0.20***	0.27***
12b) Support and aggression received	0.23***	0.37***

Table 2. TauKr correlations concerning grooming, support, opposition and rank among females in GrooFiWorld. Results represent the average TauKr value of 10 runs; Significance is based on the Bonferroni correction: *=p<0.05; **=p<0.01, ***=p<0.001. [1]1 correlation (5% of 24 correlations) is considered to be a type I error.

	GrooFiWorld		†MW U test
Intensity of aggression	High	Low	
1) Support Reciprocation	0.38***	0.27***	H 95***
1a) Rank partialled out	0.37***	0.27**	H 94***
1b) Proximity partialled out	**0.32*** **	**0.20*** **	H 95***
2) Grooming for Support Received	0.36***	0.29***	H 95***
2a) Rank partialled out	**0.30*** **	0.29***	H 58 NS
2b) Proximity partialled out	**0.26*** **	**0.21*** **	H 83*
3) Support for Grooming Received	0.29***	0.36***	L 85**
3a) Rank partialled out	0.29***	0.36***	L 84**
3b) Proximity partialled out	**0.21*** **	**0.27*** **	L 80*
4) Opposition reciprocation	-0.11**	0.29***	L 100***
4a) Rank partialled out	**0.00**	0.29***	L 100***
4b) Proximity partialled out	-0.14**	**0.22*** **	L 100***

Table 3. **Tau Kr correlations for reciprocation and exchange of support among females in GrooFiWorld when partialling out rank and proximity.**Values represent the average over 10 runs; In **bold:** results that differ significantly from the non-partial correlation. P-value based on the Bonferroni correction: *p=<0.05; **p=<0.01, ***p=<0.001.† MW U test = Mann-Whitney U test between high and low intensity of aggression , H= higher at high intensity of aggression; L = higher at low intensity of aggression; NS= not significant; n_1=10, n_2=10.

	GrooFiWorld		GrooFiWorld without immediate reciprocation	
Intensity of Aggression	High	Low	High	Low
1) % of fights involving coalitions	10%	7%	7%	7%
2) Conservative coalitions %	71%	29%	64%	28%
3) Bridging coalitions %	21%	27%	26%	27%
4) Revolutionary coalitions %	8%	44%	10%	45%
5) Reciprocation of support (TauKr)	0.38***	0.27***	0.18***	0.20***
6) Grooming for Support Received (TauKr)	0.36***	0.29***	0.35***	0.28***
7) Support for Grooming Received (TauKr)	0.29***	0.36***	0.29***	0.35***
8) Opposition given and opposition received	-0.11**	0.29***	-0.07**	0.28***
9) Opposition given and grooming received	0.31***	0.41***	0.34***	0.40***
10) Grooming given and opposition received	0.43***	0.35***	0.43***	0.34***
11) Support given and opposition given	0.13***	0.28***	0.17**	0.26***
12) Support given and opposition received	0.20***	0.27***	0.19***	0.26***

Table 4. Coalition patterns after controlling for immediate reciprocity. Patterns among females. Results represent the average over 10 runs; P-value based on the Bonferroni correction: *p=<0.05; **p=<0.01, ***p=<0.001.

Table 5.

Sex	Females	Females	Females
Intensity of Aggression	High	Low	[1]High
Number of females; males	8;2	12;5	24;6
Base of risk aversion; number of actual decisions	2; ~2	2; ~1	5; ~5
Dominance Style			
1) Gradient of the hierarchy (CV)[2]	0.81	0.37	0.71
2) Unidirectionality of aggression (TauKr)	-0.44*	0.46***	-0.45***
3) Time spent fighting (%)	14	18	9
4) Relative female (male) dominance	0.17	0.00	0.17
5) Mean distance among all group members	16	18	24
6) Centrality of dominants (Tau)	-0.59*	-0.03	-0.47***
Affiliative patterns			
7) Time spent grooming (%)	16	20	26
8) Conciliatory Tendency	15	30	14
9) Grooming reciprocation (TauKr)	0.35**	0.48***	0.57***
10) Grooming up the hierarchy (TauKr)	0.45**	[3]**0.10***	0.29***
11) Grooming partners of similar ranks (TauKr)	0.31*	-0.11	0.23***
12) Reconciliation with valuable partners	0.44**	0.02	0.36***
Coalition patterns			
13) % of fights involving coalitions[4]	8	7	8
14) Conservative coalitions %	63%	29%	85%
15) Bridging coalitions %	25%	26%	13%
16) Revolutionary coalitions %	12%	45%	2%
Jonckheere-Terpstra test (C>B>R)	JT=5***	JT=222 NS	JT=0***
Triadic awareness patterns			
17) Recipient < Target < Supporter	63%	24%	87%
18) Support given to 'friend'	61%	**54%NS**	82%

Table 5 cont.

TauKr Correlations			
19) Support Reciprocation (TauKr)	0.37**	0.23**	0.37***
20) Grooming for Support Received (TauKr)	0.43**	0.25**	0.30***
21) Support for Grooming Received (TauKr)	0.21*	0.31**	0.23***
22) Opposition given and opposition received	-0.31*	0.25***	-0.42***

Table 5. Sensitivity analysis of parameters of the complete model. Patterns among females in GrooFiWorld for several group sizes, sex ratios and degrees of risk aversion. Results represent the average over 10 runs; P-value based on the Bonferroni correction: *p=<0.05; **p=<0.01, ***p=<0.001. In **bold:** results that differ from the full model (in Table 3). [1]At low intensity of aggression a risk aversion base of 5 implies an actual number of decisions to avoid risks of ~1 (see table 2). [2]Among all individuals. [3]1 correlation (5% of 24 correlations) is considered to be a type I error. [4]For a social facilitation of 10%, the percentage of fights involving coalitions is ~4% and all coalition patterns among females are retained (results not shown, data available on request).

Chapter 4

Interchange of Grooming and Opposition: Testing Predictions from the GrooFiWorld Model

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This chapter is currently under review

Abstract

In primates, the mechanisms underlying reciprocity and interchange of support, grooming and opposition (also known as contra-support) are debated. One possibility is that individuals keep records of acts received from each partner and pay back goods or services accordingly, i.e. 'calculated reciprocity'. However, calculated reciprocity seems unlikely when considering cognitive limitations of primates, especially long-term memory. In a former paper based on a computer model (Hemelrijk and Puga-Gonzalez, 2012), we showed that the usual patterns of reciprocation and interchange of grooming and support emerge without record-keeping by individuals due to proximity and social-spatial structuring. The model, called GrooFiWorld, also generated other counter-intuitive predictions: that individuals interchange opposition for receipt of grooming and grooming for receipt of opposition. In GroofiWorld, individuals tend to remain together and when nearby another they may attack if their chance of winning is high, otherwise, they may groom; support and opposition in fights emerge when incidentally after a fight between two individuals, a third nearby individual attacks one of the former opponents. We tested the novel predictions in empirical data of three species of macaques (*M. radiata, M. assamensis, and M. mulatta*), and confirmed that females oppose more often those by whom they are groomed more and vice versa. Even though we cannot discard sophisticated cognition, our results suggest that patterns of reciprocation and interchange in macaques may be dependent on the social-spatial structuring of the group.

Introduction

Although a great deal of research in primates has documented long-term reciprocity of grooming (Hemelrijk & Ek 1991; Hemelrijk & Luteijn 1998; Watts 2002; Schino et al. 2003; Schino et al. 2007; Frank & Silk 2009; Gomes et al. 2009; Schino et al. 2009) and support (Watts 2002; Schino et al. 2007), their interchange (Hemelrijk & Ek 1991; Hemelrijk et al. 1999; Watts 2002; Schino et al. 2007), and the interchange of food for sex or other services (Hemelrijk et al. 1992; Hemelrijk et al. 1999; Gomes & Boesch 2009) the cognitive and behavioural mechanisms underlying reciprocity remain unclear. One possibility is that individuals keep track of the number of acts given to and received from each partner, so-called 'calculated reciprocity' (de Waal & Luttrell 1988; Frank & Silk 2009; Gomes & Boesch 2009). However, due to memory limitations, calculated reciprocity seems unlikely because individuals are required to keep track of interactions over a long period of time (Stevens & Hauser 2004). Therefore, several recent studies have investigated whether individuals reciprocate services over short periods of time, i.e. immediate reciprocity. These studies, however, have failed to show evidence for immediate reciprocity (Schino et al. 2003; Manson et al. 2004; Schino et al. 2007; Brosnan et al. 2009; Frank & Silk 2009; Schino et al. 2009; Jaeggi et al. 2013). Further, calculated reciprocity is supposed to be hardest when individuals reciprocate not only support but also opposition in fights, i.e. contra-support (de Waal & Luttrell 1988). Opposition in fights happens when during or immediately after a fight (e.g. between *A* and *B*) a new individual (e.g. *C*) attacks one of the former opponents (e.g. *A*); here, *C* supports *B* and opposes *A*. It has been suggested that the fact that reciprocation of opposition occurs in chimpanzees but not in monkeys is an indication of higher cognitive abilities in chimpanzees (de Waal & Luttrell 1988; but see, Silk 1992).

However, in a previous study, we have shown with the help of an individual-based model that sophisticated cognition may not be necessary for reciprocation of opposition. Neither is record- keeping needed for reciprocation of grooming or support or for their interchange (Hemelrijk & Puga-Gonzalez 2012). In the model, individuals group and when they are nearby others, they may fight or

groom them. They attack others when their chance of winning is high; otherwise, they tend to groom. They have a higher tendency to groom others when they are more anxious themselves, and grooming reduces their anxiety (Hemelrijk 1999a; Hemelrijk 2000a; Puga-Gonzalez et al. 2009). Support and opposition in fights happen by accident when immediately after a fight a nearby individual incidentally attacks one of the former opponents (Hemelrijk & Puga-Gonzalez 2012). Individuals in the model reciprocate opposition as a side effect of a shallow hierarchy (leading to bidirectionality of aggression) and frequent proximity to the same partners. Thus reciprocation of opposition is a subset of bidirectionality of aggression (Hemelrijk & Puga-Gonzalez 2012). Furthermore, in the model Individuals reciprocate grooming and support, and interchange grooming for support received and support for grooming received (Hemelrijk & Puga-Gonzalez 2012). In the model, these patterns disappear when individuals interact with partners at random. Thus, the model suggests that the patterns observed in societies of primates may depend on the socio-spatial configuration of the group. A similar socio-spatial structure has been found in several empirical studies (Itani 1954; Imanishi 1960; Yamada 1966; Janson 1990; Hirsch 2011; Singh et al. 2011). In addition, the model generates novel predictions regarding patterns of opposition. It predicts that when females intervene in fights, they will oppose more often those females i) that they attack more during dyadic fights because there is no separate rule for opposition and thus opposition is a subset of dyadic aggression; and ii) from whom they receive more grooming because due to the spatial structure females interact more with certain partners and thus they groom and fight more among each other than with others. Besides, for the same reasons, the model also predicts that females will receive opposition more often from those partners iii) from whom they receive more attacks during dyadic fights, and iv) that they actively groom more often (Table 1) (Hemelrijk & Puga-Gonzalez 2012).

Our main aim in this study is to test these predictions using data on aggression, grooming, support and opposition in fights from three different species of macaques: bonnet (*Macaca radiata*), Assamese (*Macaca assamensis*), and rhesus (*Macaca mulatta*) macaques. Macaque species can be classified according

to dominance style which varies from extremely intolerant to extremely tolerant also referred to as ranging from grade 1 to grade 4. Rhesus macaques are considered extremely intolerant (grade 1), Assamese macaques mildly tolerant (grade 2), and bonnet macaques mildly tolerant (grade 3) (Thierry 2004). We first investigated whether in the groups of these species the patterns of social interaction were consistent with the dominant style usually attributed to them (Thierry 2004; table 1 in Puga-Gonzalez et al. 2009; Table 1 in Hemelrijk & Puga-Gonzalez 2012). Next, we tested the model-based hypotheses on patterns of opposition.

Dominance Style	**Tolerant and intolerant**
TaurKr Matrix correlations between:	
1) Opposition given and aggression given	+
2) Received opposition and received aggression	+
Interchange:	
3) Aggression given and received grooming	+
4) Received aggression and grooming given	+
5) Opposition given and received grooming	+
6) Received opposition and grooming given	+

Table 1. Predicitions arising from the GrooFiWorld model (Hemelrijk & Puga-Gonzalez 2012). The direction of the correlation is shown.

Methods

Ethical standards

All animal procedures were approved by the University of Georgia Institutional Animal Care and Use Committee and were in compliance with Indian Law.

Subjects and living conditions of study groups

We collected behavioural data on one group of Assamese macaques (*M. assamensis*), one group of rhesus macaques (*M. mulatta*), and two groups of bonnet macaques (*M. radiata*) at various locations in India. For group compositions see Table 2. Details of these study groups and our data collection procedure have been published elsewhere (Cooper et al. 2004; Cooper et al. 2007; Cooper & Bernstein 2008). Briefly, the Assamese, rhesus, and provisioned groups of bonnet macaques received food each day from humans at separate temple sites and foraged on natural vegetation. The provisioned animals moved freely around the temple site and on the surrounding hills. The group of wild bonnet macaques lived in a dry mixed deciduous forest in the Indira Gandhi Wildlife Sanctuary, fed primarily on natural vegetation, and occasionally found litter along the roadside.

Macaque Group	Number of individuals			% of counter aggression (absolute frequency of aggression)		
	Males	Females	Juveniles	All	Males	Females
Bonnet Provisioned	8	13	21	15 (918)	20 (186)	4 (345)
Bonnet Wild	5	5	8	8 (348)	0 (84)	0 (143)
Rhesus Provisioned	3	6	9	14 (245)†	0 (14)†	3 (94)†
Assamese Provisioned	14	14	29	17 (1199)†	25 (503)†	6 (202)†

Table 2. Group composition, acts of support and opposition, and counter aggression in the groups of macaques. †From (Cooper & Bernstein 2008).

Behavioural Observations

1008 h of behavioural observation were collected on Assamese macaques, from October 1997 to February 1998, and 264 h of behavioural observation on rhesus macaques, from March to May 1998. The wild bonnet macaque group was observed for 875 h from July 2000 to May 2001 and the provisioned bonnet macaque group for 907 h from November 1999 to October 2000. MAC collected the data for each group and reached 90% reliability with research assistants.

Focal animal sampling was conducted on all adult animals as well as several subadult males in each study group. Four hours per individual of focal sampling

were collected in the Assamese and rhesus groups and ten hours in the bonnet groups. During focal samples, all affiliative and agonistic interactions involving the subject as well as the identity of the initiator and recipient were recorded. Affiliative behaviour included allogroom, embrace, contact (including manual touch, passive touch, and huddle), play, muzzle touch, lip-smack, genital touch, and mount. Agonistic behaviour included silent bared-teeth display, lip-grin, avoid, flee, open-mouth threat, swing, lunge, charge, chase, manual contact aggression, bite, and severe bite. Our ethogram was derived from previous research on macaques (Bertrand 1969; de Waal & Luttrell 1989; Petit & Thierry 1992). All agonistic responses involving a third-party were recorded indicating the direction of support. Before the start of each focal sample, the identity of each adult and subadult individual in view and its distance from the focal subject was recorded. Distances were defined as <5 m, 5-25 m, and >25 m. The occurrence and direction of agonistic behaviour and grooming were also recorded *ad libitum*. In the Assamese and rhesus groups *ad libitum* data on coalitions were limited to adult animals, whereas in the bonnet macaque groups *ad libitum* data included adults, sub-adults, and juveniles.

We combined data from focal animal sampling and ad libitum sampling to construct matrices of the direction of behaviour because differences in visibility should not alter the direction of behaviour. We constructed directional matrices for the following activities: grooming, aggression, counter aggression, submission, support, opposition. From the data of individuals in view at the start of each focal sample a visibility matrix was constructed. This matrix was used to correct for opportunity to support or oppose (see statistical analysis). Dominance hierarchies were constructed from the direction of all submissive interactions including silent bared-teeth display, avoid, and flee. We defined counter aggression as events in which the recipient of aggression responded immediately to the original aggressor with any form of aggressive behaviour.

Statistical analysis

In order to test for reciprocation and interchange, matrix correlations were computed by means of the Tau-Kr correlation as described by Hemelrijk (1990a). According to this method, reciprocity and interchange occurs when each individual directs more often acts to those partners from whom it receives more frequently acts in return. The TauKr test involves correlations between the rows of two matrices by means of Kendall's statistic of which values are summed over all rows (Hemelrijk 1990a). The probability of the observed value is calculated using Mantel's (1967) permutation procedure. The level of significance was calculated using 2000 permutations. We chose this method because it is frequently used in studies of animal behaviour, especially primates. We tested for reciprocity and interchange of social behaviours by correlating an actor and a receiver matrix; whether social behaviours were directed up the hierarchy by correlating an actor matrix with a matrix of rank of the partner (filled with the ranks of individuals); and whether grooming was directed towards partners of similar rank by correlating an actor matrix with a matrix of partners of similar rank (filled with zeros apart from the first and second closest partners in rank which are indicated as 1's). Because rows that include only zeros in both matrices are excluded, some correlations were not possible to compute because of the small sample size. These are indicated as not available, NA.

Matrices of support were corrected for opportunity to support, i.e. the total number of agonistic interactions in which an individual was involved and thus could have been supported by another. Since opportunities to support another depend on individuals being in visual proximity during an agonistic interaction, we first calculated the proportion of agonistic interactions in which a dyad of individuals may have been in visual proximity to other group members. For doing so, we created a symmetrical matrix of visibility, i.e. proportion of focal samples in which a dyad of individuals was in visual proximity to others. Then, by multiplying a symmetrical matrix of total agonistic interactions by the symmetrical matrix of visibility, we created an opportunity matrix. Finally, matrices of support were

corrected for opportunity by dividing them by the opportunity matrix. The same was done to correct the matrix of opposition for opportunity.

To increase sample size and thus the power of the statistical analysis, in the groups of bonnet macaques we included coalitions in which the target or beneficiary was a sub-adult or a juvenile. In the groups of Assamese and rhesus macaques we only analyzed coalitions that included three adults because we lacked the necessary data to correct for opportunity to support or oppose individuals when juveniles were involved.

We used the Fisher combination test for independent samples to test for the significance of the predicted behavioural patterns in all macaque groups combined. Because we tested predicted patterns, we used a one-tailed test.

Results

Predictions from primate literature

As is typically found in societies of primates (Hemelrijk & Puga-Gonzalez 2012), in our study females reciprocated grooming and support and interchanged grooming for support and support for grooming (1-2, 5-6 in Table 3).

Unexpectedly, the provisioned group of bonnet macaques showed traits of an intolerant dominance style rather than a tolerant one: grooming was directed up the hierarchy and aggression and opposition were unidirectional (3-4, 7 in Table 3). Also, similar to females in the Assamese and rhesus groups, females in the provisioned and wild groups of bonnet macaques showed a low proportion of counter-aggression (Table 2). Thus, our groups of bonnet macaques resembled intolerant species. Therefore, we combined their data with those of Assamese and rhesus groups for further analysis.

In the combined data set, we found that females directed grooming up the dominance hierarchy and towards individuals of similar rank, and aggression and opposition were unidirectional (3-4, 7-8 in Table 3). These correlations are consistent with behavioral patterns described for macaques with an intolerant dominance style. Note that most of the correlations that were found to be

significant belong to the groups with the largest number of individuals and greatest number of behavioural acts (Assamese and provisioned Bonnet macaques). In the other groups, the lack of significance was due to the low number of individuals, social interactions or both.

Predictions of the model

Our empirical data confirmed the model-based predictions on opposition. In the combined data set, at a group level opposition was correlated with dyadic aggression; active grooming was positively correlated with the receipt of aggression and of opposition; and aggression and opposition were both correlated with the receipt of grooming (Table 4).

Discussion

Consistent with previous studies, our results indicate that female macaques reciprocated grooming and support and interchanged grooming for support and support for grooming. Further, our empirical findings are in line with the new predictions from our individual-based model (Hemelrijk & Puga-Gonzalez 2012). We showed that female macaques: A) attacked more often those whom they opposed more frequently and received more often opposition from those from whom they received more frequently attacks during dyadic fights; B) groomed more often those individuals from whom they received aggression more often and attacked more frequently those from whom they received more often grooming; and C) groomed more often those from whom they received more frequently opposition and opposed more often those from whom they received more often grooming. In the model, these patterns emerge as a result of socio-spatial structure of the group: because the spatial structure of the group is relatively stable, individuals in the model usually groom, fight, support and oppose the same individuals over time causing the emergence of the correlations (Hemelrijk & Puga-Gonzalez 2012). This is corroborated by the fact that correlations in the model disappear when individuals interact with partners selected randomly (Hemelrijk & Puga-Gonzalez 2012). In our empirical data these behavioural patterns may emerge

	Macaque group				Fisher combination test		
	Assamese Provisioned	**Rhesus Provisioned**	**Bonnet Wild**	**Bonnet Provisioned**	**χ^2 (direction)**	**d.f.**	**†Expected direction**
Number of females	14	6	5	13			
Total acts in matrix of:							
Grooming	1618	573	460	2378			
Aggression	202	94	105	342			
Support	24	12	27	76			
TauKr matrix correlations between:							
1) Grooming given and its receipt	0.47*** (0.00)	0.27 (0.08)	-0.03 (0.59)	0.23** (0.00)	33.21*** (+)	8	+
2) Support given and its receipt	NA	NA	0.63* (0.03)	0.05 (0.26)	10.08* (+)	4	+
3) Opposition given and its receipt	NA	NA	NA	-0.24** (0.00)	9.54** (-)	2	-
4) Aggression given and its receipt	-0.32** (0.00)	-0.32* (0.03)	NA	-0.41*** (0.00)	36.40*** (-)	6	-
5) Grooming given and received support	0.71** (0.00)	-0.08 (0.64)	0.23 (0.19)	0.10 (0.08)	20.63** (+)	8	+
6) Support given and received grooming	0.39* (0.05)	0.09 (0.32)	0.28 (0.12)	0.08 (0.14)	16.39* (+)	8	+
Other correlations:							
7) Grooming given and rank of partner	0.1 (0.11)	-0.02 (0.56)	0.00 (0.55)	0.22* (0.01)	15.74* (+)	8	+
8) Grooming given and partners of similar rank	0.30** (0.00)	-0.05 (0.56)	0.00 (0.58)	0.09 (0.17)	15.92* (+)	8	+

Table 3. Patterns of grooming, aggression, and agonistic support in adult female macaques studied with matrix TauKr correlations and Fisher combination test. The TauKr coefficients (P-values in the predicted direction) are shown. NA: not available due to insufficient data. *p<0.05; **p<0.01; ***p<0.001. †Expected direction based on patterns found in empirical studies of macaques.

in a similar way, i.e. through socio-spatial structuring (Hemelrijk & Puga-Gonzalez 2012). In fact, evidence for similar patterns of social interaction was recently demonstrated in groups of Barbary and Japanese macaques. Here, adult female Japanese macaques directed more grooming to those partners by whom they were attacked more often and adult female Barbary macaques received more grooming from those whom they attacked more frequently (Schino et al. 2005; Carne et al. 2011).

Proximity has already been mentioned as a possible cause of patterns of support and interchange in studies of several primate species; but because correlations remain significant after partialling out proximity, researchers have concluded that proximity is not the causal factor (de Waal & Luttrell 1988; Hemelrijk & Ek 1991; Gomes & Boesch 2009). Interestingly, the model shows that partial correlations are not sufficient to eliminate the effects of proximity. In the model correlations remain significant after proximity has been partialled out. Only when we omit proximity from the model in a different way, namely by making individuals interact with others chosen at random, correlations disappear (Hemelrijk & Puga-Gonzalez 2012). Because partialling out proximity is insufficient to eliminate its effect in the model, previous analyses of empirical data may have underestimated the effects of proximity.

Furthermore, several empirical studies have shown that proximity is a critical factor determining the distribution of social behaviour. For instance, Ferreira et al. (2006) found that in capuchin monkeys individuals tended to support those that were in close proximity and several studies of reconciliation have shown that closer proximity between former opponents after a fight is associated with increased reconciliation (Matsumura 1996; Call 1999; Majolo et al. 2009).

There are several reasons why we think reciprocity and interchange are unlikely to be calculated by primates. First, within the framework of calculated reciprocity it is unlikely that individuals groom others for the receipt of opposition. Second, limitations in the long-term memory of monkeys make calculated reciprocity difficult (Stevens & Hauser 2004). Even for immediate interchange or reciprocity there is no conclusive evidence. For example, Schino and co-authors

(2007; 2009) found no evidence that the receipt of grooming increased the short-term probability of paying back by supporting or grooming a partner. Experiments with chimpanzees have shown that individuals fail to provide more food to partners from whom they received food previously (Brosnan et al. 2009). Similarly, Gilby et al. (2010) found no evidence of interchange in the short-term; males sharing meat with estrous females did not increase their mating probability (Hemelrijk et al. 1999). Third, as mentioned above, partialling out a variable is insufficient to eliminate its effect (Hemelrijk & Puga-Gonzalez 2012), thus, cases of supposed calculated reciprocity or interchange may be flawed for this reason.

Recently, Schino and Aureli (2009) have proposed emotional bookkeeping as an alternative mechanism to calculated reciprocity. Emotional bookkeeping refers to the emotional attachment individuals develop with each other which may lead to an interchange of beneficial acts (Schino & Aureli 2009). In a new version of our individual-based model, called 'FriendsWorld', we have shown that with some extra cognition, namely by individuals intentionaly trying to keep proximity to their 'friends' (i.e. those individuals with whom ego is more often involved in grooming) the patterns of reciprocation and interchange of grooming and support emerge even stronger than before (see Chapter 6).

Generalized reciprocity is another cognitively simpler alternative to calculated reciprocity. Here, an individual supports another one only if it has received support previously, independently of the identities of the actor and receiver. Thus, generalized reciprocity does not require memory of the identity and past behaviour of the partner and may rely on a simple rule such as "support anyone if previously supported by someone" (van Doorn & Taborsky 2012). This mechanism has recently been the focus of several theoretical studies and it has been shown that for reciprocity to arise, individuals must have differentiated relationships (Hamilton & Taborsky 2005; Rankin & Taborsky 2009; Barta et al. 2011; van Doorn & Taborsky 2012). Although testing for the emergence of generalized reciprocity in the GrooFiWorld model is beyond the scope of this study, the model does offer a mechanism explaining the emergence of differentiated relationships, i.e. by means of the socio-spatial structuring of the group.

	Macaque group				Fisher combination test		
	Assamese Provisioned	**Rhesus Provisioned**	**Bonnet Wild**	**Bonnet Provisioned**	**χ^2 (direction)**	**d.f.**	**†Predicted direction**
Number of females	14	6	5	13			
Total acts in matrix of opposition	9	10	12	80			
TauKr matrix correlations between:							
1) Opposition given and aggression given	NA	NA	NA	0.59*** (0.00)	15.20*** (+)	2	+
2) Received opposition and received aggression	NA	0.00 (0.57)	NA	0.53*** (0.00)	16.31** (+)	4	+
3) Aggression given and received grooming	0.07 (0.20)	-0.08 (0.68)	-0.28 (0.86)	0.28*** (0.00)	18.06* (+)	8	+
4) Received aggression and grooming given	0.10 (0.09)	0.21 (0.09)	-0.10 (0.72)	0.20** (0.00)	21.67** (+)	8	+
5) Opposition given and received grooming	NA	NA	0.00 (0.53)	0.33*** (0.00)	16.45** (+)	4	+
6) Received opposition and grooming given	NA	0.00 (0.65)	-0.21 (0.82)	0.28*** (0.00)	16.47* (+)	6	+

Table 4. Testing predictions on aggression and opposition in adult female macaques studied with matrix TauKr correlations and Fisher combination test. The TauKr coefficients (P-values in the predicted direction) are shown. NA: not available due to insufficient data. *p<0.05; **p<0.01; ***p<0.001. †Model based-hypotheses from GrooFiWorld at high intensity of aggression (see table 1).

Our results were mainly due to one group, the provisioned group of bonnet macaques (Table 4). In this group all predictions of the model were statistically significant; whereas in the other three groups the correlations could either not be computed or were not significant (Table 4). The lack of significance in these groups

was likely due to 1) the low number of individuals in the group and 2) the small number of acts of opposition observed. For instance, the wild group of bonnet macaques and the group of rhesus macaques comprised only 5 and 6 adult females respectively (Table 2), and the number of acts of opposition were less than 13 in both cases (Table 4). Similarly, although the Assamese macaque group contained 14 adult females, few acts of opposition were observed (n=9, Table 4). The provisioned group of bonnet macaques had the largest sample size, in part because coalition data with juveniles were included (Table 2); however, even when juveniles were excluded, all the predicted patterns remained significant, except for the correlation between active grooming and opposition received (Table 5). Rather than omitting the groups that were smaller or comprised a low number of events, we conservatively kept data from all groups and combined them with the Fisher combination test.

Unexpectedly our study only concerned intolerant societies, because our groups of bonnet macaques showed traits consistent with an intolerant dominance style. For example, females directed grooming up the dominance hierarchy and towards individuals of similar rank, aggression and opposition were unidirectional, and the rate of counter aggression was similar to that of Assamese and rhesus macaques. Similarly, other studies indicate an intolerant dominance style in bonnet macaques. Silk (1982) showed that female bonnet macaques groomed higher ranking females more frequently than those of lower rank and that the rate of grooming among females of similar rank was higher than that among those of distant ranks. Balasubramaniam et al. (2012b) found that hierarchical steepness in bonnet macaques was similar to that found in other species of macaques classified as intolerant. In contrast, bonnet macaques have shown a tolerant dominance style on other traits such as reconciliation, kin-based social interactions, acquisition of rank by females, infant handling and male emigration (Thierry 2000; Thierry 2004). For example, the conciliatory tendency for females in the provisioned group of bonnet macaques was 39.1% (Cooper et al. 2007), and thus, within the range of tolerant macaque species (Thierry 2000; Thierry 2004).

Matrix correlations between:	TauKr
1) Opposition given and aggression given	0.53***
2) Received opposition and received aggression	0.38*
Interchange:	
3) Aggression given and received grooming	0.27***
4) Received aggression and grooming given	0.20**
5) Opposition given and received grooming	0.32**
6) Received opposition and grooming given	-0.04

Table 5. Testing predictions on aggression and opposition in adult female macaques of the Bonnet provisioned group omitting data of juveniles. The TauKr coefficient values are showed. *p<0.05; **p<0.01; ***p<0.001.

Although our model does not represent the great complexity of primate cognition, it reproduces and predicts many different behavioural patterns of primate societies and, herewith, the model has a broad explanatory power. For instance, it has predicted that female dominance over males increases with the percentage of males in the group which was confirmed empirically (Hemelrijk et al. 2008b). Affiliative patterns that emerge in the model resemble those found in tolerant and intolerant primate species (Puga-Gonzalez et al. 2009). It also reproduces patterns of reciprocation and interchange of grooming and support and generates predictions for types of coalitions (i.e. conservative, bridging and revolutionary ones) and of triadic awareness in the choice of coalition partners (Hemelrijk & Puga-Gonzalez 2012). In the present study we provide empirical support for novel predictions generated by the model, namely that individuals oppose more those partners they attack more and exchange grooming for the receipt of opposition and vice versa. Therefore, processes underlying these patterns in real primates may be similar to those in the model. To investigate this, more empirical studies are needed.

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Chapter 5

Empathy versus Parsimony in Understanding Post-Conflict Affiliation in Monkeys: Model and Empirical Data

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Abstract

Post-conflict affiliation between former opponents and bystanders occurs in several species of non-human primates. It is classified in four categories of which affiliation received by the former victim, 'consolation', has received most attention. The hypotheses of cognitive constraint and social constraint are inadequate to explain its occurrence. The cognitive constraint hypothesis is contradicted by recent evidence of 'consolation' in monkeys and the social constraint hypothesis lacks information why 'consolation' actually happens. Here, we combine a computational model and an empirical study to investigate the minimum cognitive requirements for post-conflict affiliation. In the individual-based model, individuals are steered by cognitively simple behavioural rules. Individuals group and when nearby each other they fight if they are likely to win, otherwise, they may groom, especially when anxious. We parameterize the model after empirical data of a tolerant species, the Tonkean macaque (*Macaca tonkeana)*. These parameters concerned group size, sex ratio, intensity of aggression, relative frequency of grooming and aggression, female dominance, and the distribution of dominance values. We find evidence for the four categories of post-conflict affiliation in the model and in the empirical data. We explain how in the model these patterns emerge from the combination of a weak hierarchy, social facilitation, risk-sensitive aggression, interactions with partners close-by and grooming as tension-reduction mechanism. We indicate how this may function as a new explanation for empirical data.

Introduction

Cognitively complex explanations have been given for many aspects of social behaviour in primates. For instance, post-conflict affiliation between former opponents of a fight and bystanders is usually referred to as 'consolation' and 'appeasement '. Whether the assumption of high cognition underlying such social behaviour is justified is unsure, but it appears difficult to find cognitively simpler explanations. Here we use a combination of a computer model 'GrooFiWorld' based on self-organisation (Puga-Gonzalez et al. 2009) and empirical data of a tolerant species of macaques, Tonkean macaques (*Macaca tonkeana*) to investigate what mechanisms may underly the occurrence of four forms of post-conflict affiliation between former opponents of a fight and bystanders, namely 'appeasement', which is when the former aggressor receives affiliation, 'consolation' when the former victim receives it, 'solicited appeasement' when the former aggressor solicits affiliation from a bystander (i.e. it initiates affiliation), and 'solicited consolation' when the former victim solicits it. In order to avoid the use of such anthropomorphic terms, we will refer to these categories of interaction as post-conflict affiliation that is received or solicited by former aggressors and victims.

Several functions have been suggested for these postconflict interactions: relieving stress, reducing the risks of redirected aggression, recruiting support, strengthening bonds with valuable partners (i.e. individuals with whom they groom the most), and substituting reconciliation (Das 2000; Palagi et al. 2006; Koski & Sterck 2007; Fraser & Aureli 2008; Koski & Sterck 2009; Romero et al. 2009; Romero et al. 2011). As to the cognitive mechanisms underlying them, special emphasis has been put on the post-conflict affiliation directed to the victim, i.e. 'consolation'. Consolation was found to occur in apes but not in monkeys. This result has been interpreted as indicating a limitation of the cognitive capacity of monkeys, i.e. the cognitive constraint hypothesis (de Waal & Aureli 1996). According to this hypothesis, 'consolation' happens if a bystander recognizes that the victim is in distress and tries to alleviate its distress. The absence of 'consolation' in monkeys has been attributed to their lack of 'cognitive empathy' (i.e. the capacity to understand the emotional state of others, Preston & de Waal

2002). 'Consolation', however, has recently been found in dogs (*Canis familiaris*) (Cools et al. 2007), wolves (*C. lupus*) (Palagi & Cordoni 2009), horses (*Equus caballus*) (Cozzi et al. 2010), rooks (*Corvus frugilegus*) (Seed et al. 2007), and in two species of monkeys (Call et al. 2002; McFarland & Majolo 2012) from which it is known that their cognitive abilities are less developed than those of apes. Thus, whether cognitive empathy is a prerequisite for the occurrence of 'consolation' is questionable. The social constraint hypothesis is more parsimonious. It states that the occurrence of 'consolation' may be related to a difference in the risks of aggression in different societies when approaching a former opponent (de Waal & Aureli 1996). In species with a tolerant dominance style the risks of receiving aggression on approaching are lower than in species with an intolerant dominance style, making such affiliation more likely. In line with this is the fact that the only monkey species in which consolation has been confirmed are species that are tolerant, namely the stump-tailed macaque (*M. arctoides*) and Barbary macaque (*M. sylvanus*) (de Waal & Luttrell 1989; Call et al. 2002; Thierry & Aureli 2006; McFarland & Majolo 2012). This hypothesis, however, does not explain why such affiliative postconflict behaviour happens in the first place.

In the present study, we are interested in the minimal cognitive abilities required to generate these four categories of post-conflict interaction. To investigate this, we chose the individual-based model, 'GrooFiWorld' because this model has already reproduced many complex behavioural patterns that resemble those of primates. For example, in the model individuals reciprocate both grooming and support and interchange grooming for support (Hemelrijk & Puga-Gonzalez 2012) even though they do not keep record of acts given and received as has been assumed to be necessary (de Waal & Luttrell 1988). Moreover, individuals reconcile fights, especially with valuable partners, and do so more often in tolerant than in intolerant societies, despite the fact that they lack memory of former opponents and a conciliatory disposition (Puga-Gonzalez et al. 2009). Besides, in this model individuals lack the cognitive abilities thought necessary to display consolation, i.e. individuals lack cognitive empathy and the motivation to 'console'. Instead, they behave according to simple rules of thumb: they tend to group and

when they are near another individual they fight if their chance of winning is high; if they decide not to fight, they consider grooming especially when they are anxious (Puga-Gonzalez et al. 2009; Hemelrijk & Puga-Gonzalez 2012).

We compare the frequency and distribution of post-conflict affiliation in the model to empirical data of a monkey species known for its high level of social tolerance, relaxed dominance relationships and its great propensity for affiliative contacts and appeasement *i.e.* the Tonkean macaque (*Macaca tonkeana*) (Petit & Thierry 1994; Demaria & Thierry 2001; De Marco et al. 2010; De Marco et al. 2011). Furthermore, because several empirical studies have shown that individuals who groom each other more often also are more often involved in consolation (Das 2000; Palagi et al. 2006; Fraser et al. 2008; Romero & de Waal 2010; McFarland & Majolo 2012), we also study the relation between consolation and 'valuable partners' in the model and empirical data.

Because of the high level of social tolerance in Tonkean macaques, we expect to find the four categories of post-conflict affiliation. The behavioural mechanisms we use to explain these patterns in the model may also hold for empirical data.

Methods

Ethics Statement

This study complied with French laws under the permission N°67-100 given by the French Agricultural Department. The group ranged semi-free in a wooded park of approximately one acre surrounded by fences, which included an indoor cage (Thierry 1985). Monkey commercial diet and water were available *ad libitum*. Fresh food was distributed once a week but not during observations.

Empirical study

Subjects

The study was conducted on a well-established group of Tonkean macaques at the Primate Centre of Strasbourg, France. During the period of study, the group

comprised 35 to 38 individuals, 19 adults (8 males and 11 females), 6 subadults (3 males and 3 females), 7 juveniles and 0-3 infants. Subadults were between 3 and 5 yrs old, and juveniles ranged between one and three years. All animals were present throughout the study. In the present paper we confine ourselves to females (n= 14; 11 adults and 3 subadults).

Collection and Analysis of Empirical Data

The study comprised 605 hours of observation. Aggressive behaviour included chasing, lunging, slapping, grabbing, biting or fierce biting; and non-aggressive behaviour included avoidance, lipsmack, screaming, or fleeing. We distinguished four different categories of post-conflict affiliation with affiliation received by former opponents from bystanders (i.e. 'consolation' and 'appeasement') and with affiliation solicited by former opponents from bystanders (i.e. 'solicited consolation' and 'solicited appeasement'). Post-conflict affiliation behaviour was recorded following de Waal & Yoshihara (1983). After an agonistic interaction, either the victim or aggressor was followed during a 5-min post-conflict period (PC). PCs were restarted if aggression recurred within 30 s after the beginning of the PC. A 5-min matched-control period (MC) of the focal individual was taken on the next possible observation day at approximately the same time. Affiliative interactions comprised: sitting in contact, allogrooming, social play, mount, embrace, gentle touch, lipsmack and bared-teeth display (Thierry et al. 1989). To compare PC and MC, we divided the periods into blocks of 10 seconds (10-s block) and recorded the block in which the first affiliative contact between former opponents occurred. PC-MC pairs were called 'attracted' when the affiliative contact occurred earlier in PC period than in MC period; 'dispersed' when it occurred earlier in MC than in PC; and 'neutral' when it occurred during the same 10-s block in MC and PC period or when no contact occurred in either PC or MC period (de Waal & Yoshihara 1983). To calculate the affiliative tendency we used the improved formula for measuring conciliatory tendency: number of attracted pairs minus dispersed pairs divided by the total number of pairs (for an example of the calculation see appendix) (Veenema et al. 1994). A total of 251 PC-MC pairs were collected, that consisted of

168 and 83 PC-MC pairs for aggressors and victims respectively (outdoor and indoor cases were merged into one sample). We compare the rank of aggressors with those of the victims by means of the Mann-Whitney U-test. The dominance rank of each individual was calculated based on the average dominance index (Hemelrijk et al. 2005).

Matrix correlations

We used matrix TauKr correlations (Hemelrijk 1990a) to test for reciprocity of post-conflict affiliation and to test whether former opponents solicited or received more affiliation from those bystanders: 1) from whom they also received grooming more frequently; 2) to whom they also directed grooming more frequently; 3) with whom they were also involved in grooming more frequently. For further details, see Appendix.

Modelling study

The model GrooFiWorld

A full description of the model can be found in the appendix and chapters 2 and 3. Here we only present a summary. In the model, individuals tend to group, compete and affiliate. The effects of winning and losing a fight are self-reinforcing (Barchas & Mendoza 1984; Hogeweg 1988; Hemelrijk 1999a; Hemelrijk 2000a; Hsu et al. 2006; Setchell et al. 2008). When the risk of losing a fight is high, individuals tend to avoid it and may groom instead. The decision whether to groom or not depends on their degree of anxiety: the more anxious, the more inclined to groom. As indicated by empirical studies, individuals: 1) become more anxious after a fight (Aureli 1997; Das et al. 1998; Silk 2002b); 2) reduce their anxiety when receiving affiliative behaviour (i.e. grooming) and to a lesser degree when actively grooming (Das et al. 1998; Aureli et al. 1999; Shutt et al. 2007); and 3) increase their motivation to groom when they have not been receiving grooming for some time, and decrease their motivation to groom after giving or receiving grooming (Keverne et al. 1989; Schino & Troisi 1992; Graves et al. 2002). Individuals are activated in random order; however, when an individual is spatially close to a fight (i.e. within the radius of

social facilitation, see Appendix table 1) then its chances of being activated earlier increase. Below, we describe the parameters in the model, and the way data were collected and analysed, post-conflict affiliation tendencies were measured, and experiments were done.

Parameters

We kept most of the parameter values the same as in our previous studies (chapters 2 and 3, appendix table 1) and tuned other parameters of the model to those of empirical data regarding group size (25 individuals), sex ratio (14 females, 11 males), intensity of aggression (a low value), relative frequency of grooming and aggression (4:1), female dominance (0.48) (Hemelrijk et al. 2008a), and the distribution of dominance values (Hemelrijk et al. 2005). The distribution of the dominance values we calculated by filling in dominance values between the highest and lowest dominance in the model using dominance indices from empirical data (Hemelrijk 1999a; Hemelrijk et al. 2005). For results of the model with different ratios of the frequency of grooming versus fighting see table 2 in appendix.

Experiments in the Model

To understand what caused the patterns of post-conflict affiliation in the model, we manipulated it in four different ways. First, we switched off 'social facilitation'. Social facilitation implies that an individual located close to a fight increases its likelihood of being activated next (for details see appendix). Second, we investigated the role of interactions being based on proximity by making individuals interact with partners chosen at random. Third, we switched off the increase of anxiety after a fight in the former opponents. Fourth, we made grooming independent of anxiety; thus, when individuals decided that it was too risky to fight, we made them decide by chance whether or not to groom their partners. In all experiments, the average number of interactions per individual and the relative frequency of grooming and fighting were kept the same as in the complete model.

Data collection

Every run consisted of 350 periods and each period consisted of 500 activations (i.e. group size (n=25) multiplied by 20). Data were collected from period 200 to 350 to exclude any bias caused by transient values. For each activation, we recorded the spatial position and heading of each individual. With respect to fighting we recorded the identity of the winner and loser and with respect to grooming that of the actor and receiver. We ran 10 independent replicas. The results are shown as the average value of the statistic over 10 runs. Their combined probability is based on the improved Bonferroni procedure (Hochberg 1988). We used non-parametric statistics and two-tailed probabilities; however, if patterns were predicted by empirical studies, we used one-tailed probabilities.

Analysis of affiliative tendencies

We analysed the four different categories of post-conflict affiliation between former opponents and bystanders by means of the PC-MC method in the same way as has been done empirically (de Waal & Yoshihara 1983). We focused exclusively on females (n=14). As in our previous analysis of reconciliation, the length of PC and MC periods was set to the next three activations of the focal opponent after the start of the MC or PC (Puga-Gonzalez et al. 2009). One day was represented by one period of the model, i.e. 500 activations. PCs were restarted if aggression recurred within the first activation of the former opponents after the start of the PC. PC-MC pairs were classified as ‘attracted’, ‘dispersed’, and ‘neutral’ (see above for a definition). For an example of the calculation see appendix.

To analyse associations between Post-conflict affiliation and grooming among group members, we performed the same matrix correlations with the data of the model as we did with empirical data (see section on Matrix correlations and appendix).

RESULTS

Tonkean macaques and the GrooFiWorld model

Among female Tonkean macaques and females in the GrooFiWorld model, all four categories of post-conflict affiliation were found (Table 1). According to the MC-PC method, in both the empirical study and in the model, aggressors and victims received and solicited post-conflict affiliation at similar rates (Table 1) (for details on the calculation see collection and analysis of empirical data in methods and analysis of affiliative tendencies in appendix). Aggressors were higher in rank than victims when they solicited and received post-conflict affiliation (Mann-Whitney U-test: soliciting, empirical data: n_{Agr}=27, n_{Vct}=20, U=391, p<0.01; model: n_{Agr}=541, n_{Vct}=539, U=240671, p<0.001; receiving, empirical data: n_{Agr}= 28, n_{Vct}=10, U=195, p<0.07; model: n_{Agr}=666, n_{Vct}=656, U= 345941, p<0.001). Furthermore, in both empirical data and model, aggressors and victims received more post-conflict affiliation than they solicited, but this was significant only in the model and not in empirical data (aggressors: Wilcoxon matched-pairs for received affiliation vs solicited affiliation, in model: n=14, U=55, p=0.002; in Tonkean macaques: n=13, U=41, p=0.50. victims: Wilcoxon matched-pairs for received affiliation vs solicited affiliation, in model: n=14, U=55, p=0.002; in Tonkean macaques: n=10, U= 20, p=0.83).

	Received post-conflict affiliation from a bystander by		Wilcoxon paired test	**Solicited post-conflict affiliation from a bystander by**		Wilcoxon paired test
	Aggressor	**Victim**		**Aggressor**	**Victim**	
A) Empirical Data	12.0	11.7	n.s.	3.2	7.0	n.s.
B) GrooFiWorld	15.5	13.2	n.s.	3.5	5.4	n.s.

Table 1. Frequency of post-conflict affiliative tendencies between former opponents and bystanders in empirical data and the GrooFiWorld model. Results of the model are averaged over 10 runs. **p<0.01, *** P<0.001, n.s. = non significant.

Causes of post-conflict affiliation in the model

To understand what causes these patterns in the model we investigated the consequences of four different manipulations in the model on post-conflict affiliation (Table 2). We 1) switched off social facilitation so that individuals located close to a fight are no longer more likely to be the ones who are activated next, 2) omitted the effects of proximity by making individuals interact with partners we chose at random, 3) switched off the increase of anxiety after a fight, and 4) made grooming independent of anxiety. For further details on the manipulations see methods and appendix.

When social facilitation is switched off or when individuals choose interaction partners at random, in both cases, post-conflict affiliation is no longer received from by-standers (2-3 in table 2). This is because social facilitation induces individuals close to a fight (bystanders) to be activated next and thus, to interact with one of the former opponents. Consequently, bystanders groom former opponents sooner after a fight than during the matched-control period. In the case when interaction partners are chosen at random, former opponents no longer receive post-conflict affiliation because the likelihood that a 'bystander' grooms a former opponent during the post-conflict period is the same as in the matched control (3 in table 2).

	Receipt of post-conflict affiliation		**Solicitation of post-conflict affiliation**	
	Aggressor	**Victim**	**Aggressor**	**Victim**
1) GrooFiWorld (complete model)	15.5	13.2	3.5	5.4
Experiments in the model:				
2) No social facilitation	**0.0**	**0.0**	7.1	8.0
3) Interaction partners chosen at random	**0.0**	**-3.8**	13.7	13.7
4) No increase in anxiety after a fight	15.5	14.2	0.8	2.1
5) No Anxiety induced grooming	16.3	14.0	**0.0**	**0.0**

Table 2. Post-conflict affiliative tendencies after performing four different manipulations in GrooFiWorld (see methods). Tendencies that are 0 or negative are given in bold.

When the increase of anxiety after a fight is switched off, the solicitation of post-conflict affiliation decreases (compare 1 and 4 in Table 2), and it completely disappears when grooming is independent of anxiety (5 in Table 2). Thus, solicitation of post-conflict affiliation depends on the anxiety level of the former opponent because this influences its tendency to groom.

Social relationships in the model and empirical data

In empirical data of Tonkean macaques and in GrooFiWorld the four categories of post-conflict affiliation were more frequent among partners that groomed each other more often. The specific associations in aggressors (Table 3) and victims (Table 4) are 1) former opponents directed more post-conflict affiliation to those bystanders from whom they received more post-conflict affiliation, i.e. reciprocation, 2) former opponents solicited more frequently post-conflict affiliation from those bystanders to whom they directed more grooming, and 3) those former opponents that were involved in post-conflict affiliation with each other more frequently were also involved more often in grooming interactions with each other (1, 5, 7, 8 in Table 3 & 4). A number of correlations were significant only in GrooFiWorld: former opponents received more frequently post-conflict affiliation from those bystanders 1) from whom they received grooming more frequently, and 2) to whom they directed grooming more frequently, and 3) former opponents solicited more frequently post-conflict affiliation from those bystanders from whom they received grooming more frequently (2, 3, 6 in Table 3 & 4). In the empirical study, the data of victims were insufficient for the TauKr matrix correlations (Table 4).

DISCUSSION

In the empirical data of Tonkean macaques and in the GrooFiWorld model, we found all the four categories of post-conflict affiliation between former opponents and bystanders. The frequency and distribution of post-conflict affiliation received and solicited appeared to be similar in the empirical data and the model: a) aggressors solicited and received affiliation at similar rates as victims, b) aggressors

and victims received more post-conflict affiliation than they solicited, c) they received and solicited post-conflict affiliation more frequently from those bystanders with whom they had a strong grooming relationship, and d) they reciprocated post-conflict affiliation.

	GrooFi World	Emp. Data
Aggressors received PC affiliation more frequently from those bystanders:		
1) to whom they also directed PC affiliation more frequently after a conflict	**0.07***	**0.42****
2) from whom they also received grooming more frequently in other context	**0.17****	0.09
3) to whom they also directed grooming more frequently	**0.18****	0.05
Aggressors solicited PC affiliation more frequently from those bystanders:		
4) from whom they received PC solicitation more frequently after a conflict	‡**0.06***	-0.13
5) to whom they directed grooming more frequently in other context	**0.19****	**0.26***
6) from whom they received grooming more frequently	**0.19****	0.07
Aggressors involved more frequently in grooming:		
7) Also received PC affiliation from each other more frequently	**0.26****	**0.39****
8) Also solicited PC affiliation from each other more frequently	**0.23****	**0.69*****

Table 3. Social relationships and post-conflict interactions between aggressors and bystanders in Tonkean macaques and GrooFiWorld. Matrix TauKr correlations: *p<0.05, **<0.01, ***p<0.001. PC= post-conflict. ‡1 correlation (5% of 16) is considered to be a type I error.

Our model suggests two mechanisms for the emergence of post-conflict affiliation: social facilitation and anxiety reduction. As regards affiliation received from bystanders ('consolation' and 'appeasement'), the model suggests that social facilitation is the main mechanism driving it. In the model, social facilitation increases the chances of bystanders to be activated and thus, bystanders are more likely to interact with former combatants soon after the fight. As regards solicited post-conflict affiliation ('solicited consolation' and 'solicited appeasement'), the model suggests that this may emerge when former combatants intend to relieve their own anxiety by grooming bystanders. Empirical evidence seems to support

both mechanisms, i.e. social facilitation and anxiety reduction. Social facilitation has been suggested to mediate post-conflict affiliation received by former opponents in Barbary macaques (McFarland & Majolo 2012). As to the reduction of anxiety, in Tonkean macaques and hamadryas baboons (*Papio hamadryas*), the increase in the rate of affiliation among bystanders after a fight has been attributed to an elevation of social tension and anxiety (Judge & Mullen 2005; De Marco et al. 2010) and in Barbary macaques victims of aggression significantly reduce their anxiety (measured as self-scratching) through soliciting consolation (McFarland & Majolo 2012).

In the empirical data and in the model aggressors solicited post-conflict affiliation at similar rates as victims did and received post-conflict affiliation also at similar rates as victims did. This is unexpected because aggressors were usually higher in rank than victims, and thus one would expect aggressors to direct less affiliation and receive more of affiliation than victims. The similarity of frequency in post-conflict affiliation between aggressor and victim was probably due to the shallowness of the dominance hierarchy. Consequently, bystanders perceive approximately the same risks when approaching dominant and subordinate individuals and thus, they groom both at similar rates during the post-conflict period.

Besides, in the model, former opponents (i.e. aggressors and victims) received more post-conflict affiliation than they solicited. This pattern emerges because after a conflict former opponents are less likely to be activated again and thus less likely to groom bystanders (i.e. solicit post-conflict affiliation). Similarly, in real monkeys, receiving post-conflict affiliation may be more frequent than soliciting because during the post-conflict period former opponents are still focused on their previous opponent rather than on bystanders.

Furthermore, in the model and in Tonkean macaques former opponents affiliated more with those bystanders with whom they had a stronger grooming relationship (Table 3 and 4). This is also found in several other primate species (Chimpanzees, Bonobos, Baboons and Barbary macaques: Fraser et al. 2008; Romero et al. 2008; Romero & de Waal 2010; McFarland & Majolo 2012; Clay & de

Waal 2013). Note that when valuable partners provide post-conflict affiliation to the former opponent, this is usually interpreted as an expression of cognitive empathy (Aureli & Schaffner 2002). In our model, however, this pattern emerges as side effect of the spatial structure of the group because individuals have a relatively stable spatial position which causes them to interact more with some partners than with others (Puga-Gonzalez et al. 2009; Evers et al. 2011; Evers et al. 2012; Hemelrijk & Puga-Gonzalez 2012). In agreement with this the correlation between post-conflict affiliation and grooming frequency disappear when individuals interact with partners at random (Appendix table 3 and 4). Note that in the model 'reconciliation' with valuable partners has emerged in a similar way: individuals are usually closer to those with whom they groom more (which are their valuable partners), and thus they groom them more often also after a fight, which is labelled as 'reconciliation' (Puga-Gonzalez et al. 2009).

	GrooFi World	**Emp. Data**
Victims received PC affiliation more frequently from those bystanders:		
1) to whom they also directed PC affiliation more frequently after a conflict	**0.10****	NA
2) from whom they also received grooming more frequently in other context	**0.17****	NA
3) to whom they also directed grooming more frequently	**0.21****	NA
Victims solicited PC affiliation more frequently from those bystanders:		
4) from whom they received PC solicitation more frequently after a conflict	0.03	NA
5) to whom they directed grooming more frequently in other context	**0.19****	NA
6) from whom they received grooming more frequently	**0.17****	NA
Victims involved more frequently in grooming:		
7) Also received PC affiliation from each other more frequently	**0.25****	NA
8) Also solicited PC affiliation from each other more frequently	**0.21****	NA

Table 4. Social relationships and post-conflict interactions between victims and bystanders in Tonkean macaques and GrooFiWorld. Matrix TauKr correlations: *p<0.05, **<0.01, ***p<0.001. PC= post-conflict; NA= not available (correlations could not be performed due to few data points).

At present, all macaque species in which 'consolation' has been confirmed are socially tolerant (stumptailed macaques: Call et al. 2002; Barbary macaques: McFarland & Majolo 2012, and Tonkean macaques: this study). This is consistent with the social constraint hypothesis, which argues that individuals from tolerant species have a higher degree of freedom in their social relationships than those from intolerant species, meaning that in tolerant species individuals can approach each other more easily (Thierry 1990; Butovskaya 2004). Indeed also in the model, the frequency of post-conflict affiliation is significantly higher at low intensity of aggression than at high intensity of aggression. However, the explanation for this difference differs from that of the social constraint hypothesis. It is identical to our earlier explanation why there is less reconciliation also at high than low intensity (Puga-Gonzalez et al. 2009). Namely, the frequency of post-conflict affiliation is lower at high intensity in the model than at a low intensity as a side-effect of the lower relative frequency of grooming to aggression at high intensity of aggression. The lower frequency of grooming to aggression is a side-effect of the spatial centrality of dominants, which is more pronounced at high than at low intensity of aggression. The spatial centrality causes dominants to meet others more often and thus interact with others more often than subordinate individuals do, because subordinates are more often located at the periphery of the group. The relative higher frequency of interactions by dominants at high intensity, cause a relatively lower frequency of grooming versus aggression.

Our model proposes an integrative theory of affiliative and aggressive behaviour of primates. One of the key traits in the model is aggression. Aggression causes the spatial structure of the group (Hemelrijk 1999a; Hemelrijk 2000a; Puga-Gonzalez et al. 2009; Evers et al. 2011; Evers et al. 2012; Hemelrijk & Puga-Gonzalez 2012) which influences the distribution of affiliative behaviour resulting in patterns such as reciprocation of grooming and support, exchange of grooming for support and support for grooming, reconciliation, and reconciliation with valuable partners (Puga-Gonzalez et al. 2009; Hemelrijk & Puga-Gonzalez 2012). When in the model intensity of aggression is high, many of the patterns that emerge resemble those found in intolerant societies: the dominance hierarchy is steep; individuals

direct grooming up the dominance hierarchy and towards individuals of similar rank; aggression and opposition (i.e. attacking one of the opponents while intervening in their fight) (de Waal & Luttrell 1988) are unidirectional; conciliatory tendency, time spent grooming and fighting are low; and female dominance over males is high (Hemelrijk 1999a; Hemelrijk et al. 2008a; Puga-Gonzalez et al. 2009). In addition, in the model individuals receive more opposition from those to whom they direct more grooming and direct more often opposition to those by whom they are groomed more frequently; these patterns are similar to empirical data of three intolerant species of macaques (Chapter 4). Remarkably, all these behavioural patterns emerge without assuming sophisticated cognition. Instead, these patterns emerge from cognitively simple behavioural rules in combination with the spatial structure of the group. The model also suggests that patterns are interconnected and depend on the dominance style (tolerant or intolerant), which is in line with the covariation hypothesis which states that social traits associate in clusters through development and evolution (Thierry 2004). The results obtained so far give us confidence that the model GrooFiWorld captures at least some essential traits of real primate societies, and it is useful as a null model for empirical studies.

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Appendix

Methods

Empirical study

Subjects and Living Conditions

The group comprised 35 to 38 individuals and 19 adults (8 males and 11 females), 6 subadults (3 males and 3 females), 7 juveniles and 0-3 infants. Subadults were between 3 and 5 yrs old, and juveniles ranged between one and three years.

The group was ranging semi-free in a wooded park of approximately one acre surrounded by fences, which included an indoor cage (Thierry 1985). Monkey commercial diet and water were available *ad libitum*. Fresh food was distributed once a week but not during observations.

Collection and Analysis of Empirical Data

Observations were conducted by the second author between 10 a.m. and 3 p.m. from September 15th to December 15th 1999 (330 hours), and from 1st October to December 15th 2000 (275 hours). Data were collected by all-occurrence sampling (Altmann 1974). Aggressors were followed during 1999 and victims during 2000. Agonistic interactions were recorded when an individual displayed aggressive behaviour to another and the receiver responded with aggressive or non-aggressive behaviour. A conflict was considered to be decided when one of the opponents unilaterally withdrew or submitted, and to be undecided when no clear signs of submission were shown by either opponent (e.g. counter-aggression). In case of polyadic conflicts, only the two initial combatants were considered for analysis. A total of 251 PC-MC pairs were collected: 213 outdoors (in the park) and 38 indoors (in a cage). Post-conflict affiliation concerned in 168 cases (outdoors and indoors) the aggressor and 83 cases (outdoors only) the victim. 14 females participated in aggressive encounters: 2 exclusively as aggressors (2 adults), 11 as aggressors and victims (8 adults and 3 subadults), and 1 as a victim exclusively (1 subadult).

Matrix Correlations

Sociometric matrices were built with data of interactions of approach and avoidance, grooming and post-conflict affiliation. Correlations between matrices were TauKr correlations and the level of significance was based on 2000 permutations (Hemelrijk 1990a; Hemelrijk 1990b). Due to the high number of correlations, significant results may arise by chance. We corrected for this by discarding the 5% of correlations with the lowest significances (Type I error) per table of results. Matrices of post-conflict affiliative tendencies were corrected for opportunity, i.e. number of fights in which individuals were involved and thus could have affiliated with bystanders. Matrices of grooming given and received excluded the cases of grooming considered as a post-conflict affiliation.

Analysis of affiliative tendencies

To analyse the affiliative tendencies we used the MC-PC method (Veenema et al. 1994). After each fight, we started the post-conflict (PC) period whose length was set to 10 min for empirical data and the next three activations of the focal opponent for the model. During the PC period we recorded the type of affiliation that happened first and this was the type of affiliation we controlled for during the MC period. For instance, if during the PC an affiliative interaction initiated by a bystander was the first to happen, during the MC we only controlled for this type of affiliation. If during the MC there was no such interaction or if the affiliation happened first in the PC than in the MC, this would be counted as an 'attracted' pair for affiliation initiated by a bystander. Note, however, that if during the MC affiliative behaviour was instead initiated by the former opponent towards a bystander, this was not counted as a dispersed pair in the affiliation initiated by former opponent to avoid double counting data. Also, if no affiliation happened during the PC, we only considered the type of affiliation that happened first during the MC (i.e. affiliation initiated by bystander or by former opponent) and labeled this pair as ‘dispersed’.

Modeling study

The model

We use an individual-based model called GrooFiWorld (see previous chapter 2). This is an extension of a previous model called Dom-World in which individuals group and compete (Hemelrijk 1999a; Hemelrijk 2000a; Hemelrijk 2005). The extension consists of grooming behaviour and that is why it is called 'GrooFiWorld' (i.e. Grooming and Fighting). The space of the 'world' is continuous, i.e. individuals are free to move in any direction. They have a certain angle of vision (*VisionAngle*) and a maximum distance of perception (*MaxView*). Individuals are provided with three behavioural tendencies: 1) to group, 2) to perform dominance interactions and 3) to display affiliative behaviour. At the start of each run, the individuals occupy random locations within a predefined circumference, *InitRadius*, the value of which is the product of a number and the number of individuals (Table 1). The individuals' activities are regulated by a timing regime in which each individual receives a random waiting time from a uniform distribution and the individual with the shortest waiting time is activated first. This regime is combined with a biologically plausible timing regime reflecting a kind of 'social facilitation' (e.g. see Galef 1988) in which the waiting time of an individual is shortened when a dominance interaction occurs close by (radius of social facilitation, Table 1). This function was implemented after the observation that in social species specific events, such as a fighting, may produce an increase in arousal of bystanders (or observers) leading to a response (Galef 1988). For instance, De Marco et al. (2010) have shown that after a fight, Tonkean macaque bystanders were more likely to increase affiliation, i.e. they became more active.

Setting Parameters in the model

Where possible we kept the same parameter values as in our previous studies (Table 1) (Hemelrijk 1999a; Hemelrijk 2000a; Puga-Gonzalez et al. 2009; Hemelrijk & Puga-Gonzalez 2012). However, to effectively reflect the social behaviour of the group of Tonkean macaques, we adjusted the settings of the model to the same group size, sex ratio, intensity of aggression, relative frequency of grooming and

aggression, female dominance (Hemelrijk et al. 2008a), and steepness of the hierarchy (Hemelrijk et al. 2005). Thus, group size was set to n=25 individuals, 14 females and 11 males. Intensity of aggression was set to low values because, among Tonkean macaques, aggression is mild, i.e. mostly consisting of threats and slaps (Thierry 2004). The relative frequency of grooming versus aggression in the group of Tonkean macaques was 10:1, which underestimates the frequency of aggression, because threats were not included. Since in the model we include also threats, we needed a lower ratio of grooming to aggression than the empirical one. To find a biologically relevant ratio, we investigated the effects of different ratios of grooming versus aggression on the frequency of post-conflict affiliative behaviour with bystanders (Table 2). This investigation showed that the frequency of post-conflict affiliative interactions increased with the relative frequency of grooming versus aggression (Table 2) and resembled empirical data most at a ratio of grooming to fighting of 4:1. Thus, we chose this ratio for our study. To adjust the relative frequency of grooming to aggression, the parameter values of increasing of anxiety (*AnxInc)* and of aversion to risk (*RiskAvers)* were increased (Table 1). After these modifications, the average distance among group members decreased dramatically from 20 to 4 units. Thus, we increased the distance over which an individual flees after losing a fight (*FleeingDistance),* the distance over which the winner of a fight chases its opponent (*ChaseDistance),* and the moving distance after grooming (*MoveAfterGroom*) (Table 1). In order to mimic the same female dominance and steepness of the hierarchy as in the empirical date, we first calculated the dominance index of each individual in our group of Tonkean macaques with the help of the matrix tester program (Hemelrijk 1990a; Hemelrijk et al. 2005). The dominance index ranged from 0 to 1, with 1 being most dominant and 0 least dominant. Next, from a simulation of the model at low intensity of aggression, we took the minimum and maximum dominance values and we distributed the empirical dominance values within this range. The individual with the maximum dominance value in the model represented the individual of the empirical data with a dominance index of 1 and the individual with the minimum dominance value represented the macaque with a dominance index of 0. The other

individuals in the model represented those macaques ranking in between these two extremes. The dominance values of these individuals were calculated based on the dominance index obtained from empirical data. For instance, in the model the individual representing a macaque with a dominance index of 0.5 got the average dominance value between the maximum and minimum. The dominance values were fixed during the whole simulation. This procedure implied automatically the same degree of female dominance relative to males and hierarchical gradient as in the empirical data. The data obtained from these simulations were used for the analyses of affiliative tendencies.

Parameter	Description	Females	Males
General Parameters			
GroupSize	Total number of individuals	25	
Sex ratio	Number of	14	11
Female Dominance	Relative position of females over males in the dominance hierarchy (Hemelrijk et al. 2008a).	0.48	
InitRadius	Predefined space at start of simulation	1.7*# Inds	1.7*# Inds
Radius of social facilitation	Radius starting from centre point between two opponents	10	10
Grouping Parameters			
PersSpace	Close encounter distance	8	8
NearView	Medium distance	24	24
MaxView	Maximal viewing distance	50	50
SearchAngle	Turning angle to find others	90°	90°
VisionAngle	Angle of field of view	90°	90°
Fighting Parameters			
InitDom	Initial Dom value	see main text 'parameters in the model'	
RiskAvers	Number of 'mental battles'	2.75	2.75
StepDom	Scaling factor for aggression intensity	0.08	0.1
FleeingDist	After losing a fight	4.5	4.5
ChaseDistance	After winning a fight	2.5	2.5
MoveAfterGroom	After grooming	0.5	0.5
Grooming Parameters			
InitAnx	Initial anxiety value	0.5	0.5
AnxInc	Increase in anxiety after every activation	1.2%	1.2%
AnxDcrGree	Decrease of anxiety of groomee	0.15	0.15
AnxDcrGrmr	Decrease of anxiety of groomer	0.1	0.1
AnxIncFight	Increase of anxiety after fighting	0.1	0.1

Table 1. Value of parameters in the model 'GrooFiWorld'.

Groom : Fight	Receipt of post-conflict affiliation		Solicitation of post-conflict affiliation	
	Aggressor	Victim	Aggressor	Victim
5:1	18.00	15.2	0.7	2.1
4:1	15.5	13.2	3.5	5.4
3:1	8.6	9.4	6.0	5.2
2:1	7.2	7.0	6.9	5.2
1:1	1.8	2.7	4.9	6.8
Empirical Data	12.0	11.7	3.2	7.0

Table 2. Effects of different ratios of the frequency of grooming versus fighting (groom:fight) on frequency of post-conflict affiliative behaviour with bystanders in the model GrooFiWorld. Results of the model are averaged over 10 runs. For comparison results of the empirical data are also shown.

GrooFiWorld with random interactions	TauKr coefficient
Aggressors received PC affiliations more frequently from those bystanders:	
1) to whom they directed PC affiliations more frequently after a conflict	-0.01
2) from whom they also received grooming more frequently also in other contexts	0.02
3) to whom they directed grooming more frequently	0.00
Aggressors solicited PC affiliations more frequently from those bystanders:	
4) from whom they received PC solicitations more frequently after a conflict	-0.02
5) to whom they directed grooming more frequently in other context	0.00
6) from whom they received grooming more frequently	0.00
Aggressors involved more frequently with each other in grooming:	
7) also received PC affiliations from each other more frequently	0.01
8) also solicited PC affiliations from each other more frequently	0.01

Table 3. The effect of random interactions among individuals (instead of interactions based on proximity) on social relationships and post-conflict interactions between aggressors and bystanders in GrooFiWorld. Matrix TauKr correlations. The values of the coefficients are the average of ten runs. PC= post-conflict.

GrooFiWorld with random interactions	TauKr coefficient
Victims received PC affiliations more frequently from those bystanders:	
1) to whom they directed PC affiliations more frequently after a conflict	0.01
2) from whom they received grooming more frequently also in other context	0.00
3) to whom they also directed grooming more frequently	-0.01
Victims solicited PC affiliations more frequently from those bystanders:	
4) from whom they received PC solicitations more frequently after a conflict	0.00
5) to whom they directed grooming more frequently in other contexts	0.01
6) from whom they received grooming more frequently	0.00
Victims involved more frequently with each other in grooming:	
7) also received PC affiliations from each other more frequently	0.02
8) also solicited PC affiliations from each other more frequently	0.01

Table 4. The effect of random interactions among individuals (instead of interactions based on proximity) on social relationships and post-conflict interactions between victims and bystanders in GrooFiWorld. Matrix TauKr correlations. The values of the coefficients are the average of ten runs. PC= post-conflict.

Chapter 6

Friendships, Reciprocation and Interchange in an Individual-Based Model

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This chapter is currently under review

Abstract

For a long time, 'calculated reciprocity' was thought to be the main mechanism driving patterns of reciprocation and interchange of social acts in primate societies. Recently, the focus on such highly cognitive mechanism has changed to more parsimonious ones like 'emotional bookkeeping' and self-organization. Emotional bookkeeping suggests that individuals that groom frequently develop a positive emotional bond, i.e. 'friendship', which elicits reciprocation and exchange of social acts with a specific partner. Individual-based models of self-organization suggest that reciprocation and interchange emerge through cognitively simple behavioural rules in combination with the socio-spatial structure of the group and proximity-based interactions. A main drawback of these models is the lack of representation of 'social bonding' among individuals, which recent evidence suggests to provide great fitness benefits to individuals. Here, we implement social bonding in an individual-based model called 'GrooFiWorld' to investigate the effects of 'friendships' on patterns of reciprocation and interchange of grooming and support. In the new model, 'FriendsWorld', individuals follow and stay in close proximity to their 'friends' (i.e. those with whom they affiliate the most), but do not interact differently with friends than with non-friends. We show that compared to GrooFiWorld, in FriendsWorld the mere act of individuals keeping proximity to friends causes individuals to interact preferentially with them and as a consequence strengthen the patterns of reciprocation and interchange. In contrast to emotional bookkeeping, this mechanism suggests that in real primates, reciprocation and interchange may not be intentional but a consequence of repeated interactions with preferred partners.

Introduction

Empirical researchers have always been puzzled about the proximate mechanisms explaining reciprocation and interchange of social services in primate societies. Initially, it was thought that 'calculated reciprocity', i.e. keeping mental records of the number of acts given to and received from each partner, was the main mechanism driving reciprocation and interchange (de Waal & Luttrell 1988). Nowadays, however, research on primate cognition has shown that due to cognitive limitations 'calculated reciprocity' seems an unlikely mechanism driving these patterns (Stevens & Hauser 2004). Thus, recently the focus on such a high cognitive mechanism has shifted to more parsimonious ones such as 'emotional bookkeeping' (Schino & Aureli 2009) and self-organization (Hemelrijk 1996b; Hemelrijk 1999a; Puga-Gonzalez et al. 2009; Hemelrijk & Puga-Gonzalez 2012).

Emotional bookkeeping suggests that individuals who interchange frequently friendly interactions (i.e. grooming), develop a positive emotional bond or 'friendship' (Schino & Aureli 2009). Such a positive emotional bond may motivate an individual to reciprocate or interchange a social act with its 'friend' (Schino & Aureli 2009). This mechanism is supposedly sufficient to maintain reciprocation and interchange over long periods of time (Schino et al. 2007; Schino & Aureli 2009).

Self-organization suggests that simple behavioural rules and local interactions are sufficient to generate complex patterns such as reciprocation and interchange. Several individual-based models have been developed to understand the complex behavioural patterns observed in societies of primates (Hemelrijk 1999a; Hemelrijk 2002b; Hemelrijk et al. 2008a; Puga-Gonzalez et al. 2009; Evers et al. 2011; Evers et al. 2012; Hemelrijk & Puga-Gonzalez 2012). Among these, the 'GrooFiWorld' model has been successful at predicting and generating parsimonious explanations for patterns of grooming, aggression, support and contra-support, and their differences between tolerant and intolerant societies of primates, especially macaques (Puga-Gonzalez et al. 2009; Hemelrijk & Puga-Gonzalez 2012; Puga-Gonzalez et al. in press; Puga-Gonzalez et al. under review). However, one of the main drawbacks of these models is the lack of representation

of 'social bonding' among individuals. Social bonding refers to the establishment of so-called friendships (Dunbar 1991; Silk 2002a; Massen et al. 2010). Friendships have recently been the focus of much empirical research because of the fitness benefits they have been shown to provide to individuals (Silk et al. 2003; Silk 2007b; Massen et al. 2010; Berghaenel et al. 2011)

In this study, we implement social bonding in the GrooFiWord model via a mechanism based on following the most frequent grooming partners (King et al. 2011). Our main aim is to investigate the effects of friendships on patterns of reciprocation and interchange of grooming and support in fights. In the new model called 'FriendsWorld' individuals develop friendships based on the frequency with which they give and receive grooming from certain others. However, in contrast to what is assumed by emotional bookkeeping, individuals in the model do not intend to reciprocate or interchange social acts with their friends, instead they only try to follow and stay in close proximity with them. This mechanism is even more parsimonious than emotional bookkeeping.

Methods

FriendsWorld is an individual-based, spatially explicit model, written in C++, as an extension of the GrooFiWorld model. The parameter values are the same as in previous versions of the GrooFiWorld model except for group size which was increased from 12 to 16 (Table 1). The model comprises a continuous two-dimensional 'world' (without borders) in which individuals are moving in all directions. Individuals have a fixed vision angle (*VisionAngle*, Table 1) and a maximum perception distance (*MaxView*, Table 1). At the beginning of each simulation, the individuals are located at random locations within a previously defined radius (*InitRadius,* Table 1), calculated by multiplying group size by an arbitrary constant. To regulate the activities of the individuals, each individual is attributed a random waiting time drawn from a uniform distribution and the individual with the shortest waiting time gets activated first (Hemelrijk 1999a; Puga-Gonzalez et al. 2009). These waiting times are combined with a biologically plausible timing regime, reflecting a kind of social facilitation, (Galef 1988) during

which an individual's waiting time is reduced when a dominance interaction occurs close by (Radius of social facilitation, Table 1). Intensity of aggression is reflected by the *StepDom* value. Fierce aggression (e.g. bites) as in intolerant primate societies is represented by high values, and mild aggression (e.g. threats, slaps) as in tolerant societies is represented by low values (Table 1). To represent sexual dimorphism, males have a higher *StepDom* value than females (Table 1) (Hemelrijk et al. 2008a). As in GrooFiWorld, in FriendsWorld individuals tend to 1) remain in a group, 2) fight, and 3) groom. Why individuals form groups (e.g. for predator avoidance) and fight (e.g. for food or mates) is not specified. Grooming reduces the anxiety of individuals (Keverne et al. 1989; Graves et al. 2002; Shutt et al. 2007).

Grouping rules

In FriendsWorld, individuals tend to follow their friends (King et al. 2011). Friends are defined as those individuals within the top quartile (25%) of ego's affiliation score (i.e. grooming given and received). Individuals have three different visual ranges: *PersSpace, NearView* and *MaxView* (Table 1). When an individual does not perceive another in its close proximity (i.e. within its *PersSpace*), it acts according to the grouping rules (Fig 1B). For instance, if an individual perceives a friend within its *NearView*, it will move one step towards it. If several friends are perceived, the individual moves towards the closest one. If no friends are perceived but other individuals are, the individual just keeps on moving (Fig 1B). When no others are perceived within *NearView*, the individual looks further away into *MaxView* (Table 1). If other individuals are perceived within *MaxView*, the individual moves towards the closest friend if available, otherwise it moves towards the closest individual (Fig 1B). If no individual is perceived within *MaxView,* the individual scans for others by turning over a *SearchAngle* (Table 1; Fig 1B).

Interaction Rules

In FriendsWorld, the interacting rules are the same as in GrooFiWorld (Figure 1A.). If the individual perceives another one within its *PersSpace*, a dominance interaction may occur. Whether or not the individual will attack depends on the

outcome of a mental battle. If the individual wins the mental battle, it will attack its partner (see Dominance Rules). However, if the individual loses the mental battle, it will consider grooming instead (see Grooming Rules).

Parameter	Description	Value
General Parameters		
GroupSize	Total number of individuals	16
Sex ratio (at high aggression intensity)	Number of males and females	13 females, 3 males
Sex ratio (at low aggression intensity)	Number of males and females	11 females, 5 males
InitRadius	Predefined radius at start of simulation	1.7* #Inds
Radius of social facilitation	Radius starting from centre point of fight	10
Grouping Parameters		
PersSpace	Close encounter distance	8
NearView	Medium distance	24
MaxView	Maximal viewing distance	50
SearchAngle	Turning angle to find others	90°
VisionAngle	Angle of field of view	120°
Dominance Parameters		
InitDom	Initial Dom Value	16 for females, 32 for males
RiskAvers	Number of 'mental battles' before attack	2
StepDom (at high aggression intensity)	Scaling factor for aggression intensity	0.8 for females, 1.0 for males
StepDom (at low aggression intensity)	Scaling factor for aggression intensity	0.08 for females, 0.1 for males
FleeingDist	After losing a fight	2
ChaseDist	Chasing distance after winning a fight	1
Grooming Parameters		
InitAnx	Initial anxiety value	0.5
AnxInc	Increase in anxiety after every activation	1%
AnxDcrGree	Decrease in anxiety in groomee	0.15
AnxDcrGrmr	Decrease in anxiety in groomer	0.1
AnxIncFight	Increase in anxiety after fighting	0.1

Table 1. Default parameter values in FriendsWorld.

Dominance Rules

Dominance interactions are modelled as in previous models (Hogeweg 1988; Hemelrijk 1999a; Puga-Gonzalez et al. 2009) and are extensions of the DoDom rules of Hogeweg (Hogeweg 1988). When individual *i* meets individual *j* in its *PersSpace*, individual *i* considers whether it will be able to win a fight against *j* by means of a 'mental battle'. During a mental battle, individual *i* compares its *Dom* value relative to that of *j*; individual *i* expects to win if its relative dominance value is greater than a random number drawn from a uniform distribution between zero and one (Equation 1). A 'mental battle' may be carried out once or several times, depending on the value of risk aversion (*RiskAvers*, Table 1). The higher the risk aversion, the more mental fights an individual must win before it actually attacks its opponent. During an actual dominance interaction, the relative *Dom* value is again compared to a randomly drawn number between zero and one; if the relative *Dom* value is higher than this random number, individual *i* wins the fight ($w_i = 1$); otherwise, it loses ($w_i = 0$) (Equation 1):

$$w_i = \begin{cases} 1 & \dfrac{DOM_i}{DOM_i + DOM_j} > RND(0,1) \\ 0 & else \end{cases} \qquad (1)$$

To represent self-reinforcing effects of victory and defeat (Hsu & Wolf 1999; Hsu et al. 2006) after a fight, the dominance value of the winner is increased, while that of the loser is decreased by the same amount respectively (Equation 2),

$$DOM_i = DOM_i + \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) * STEPDOM$$

$$DOM_j = DOM_j - \left(w_i - \frac{DOM_j}{DOM_i + DOM_j} \right) * STEPDOM \qquad (2)$$

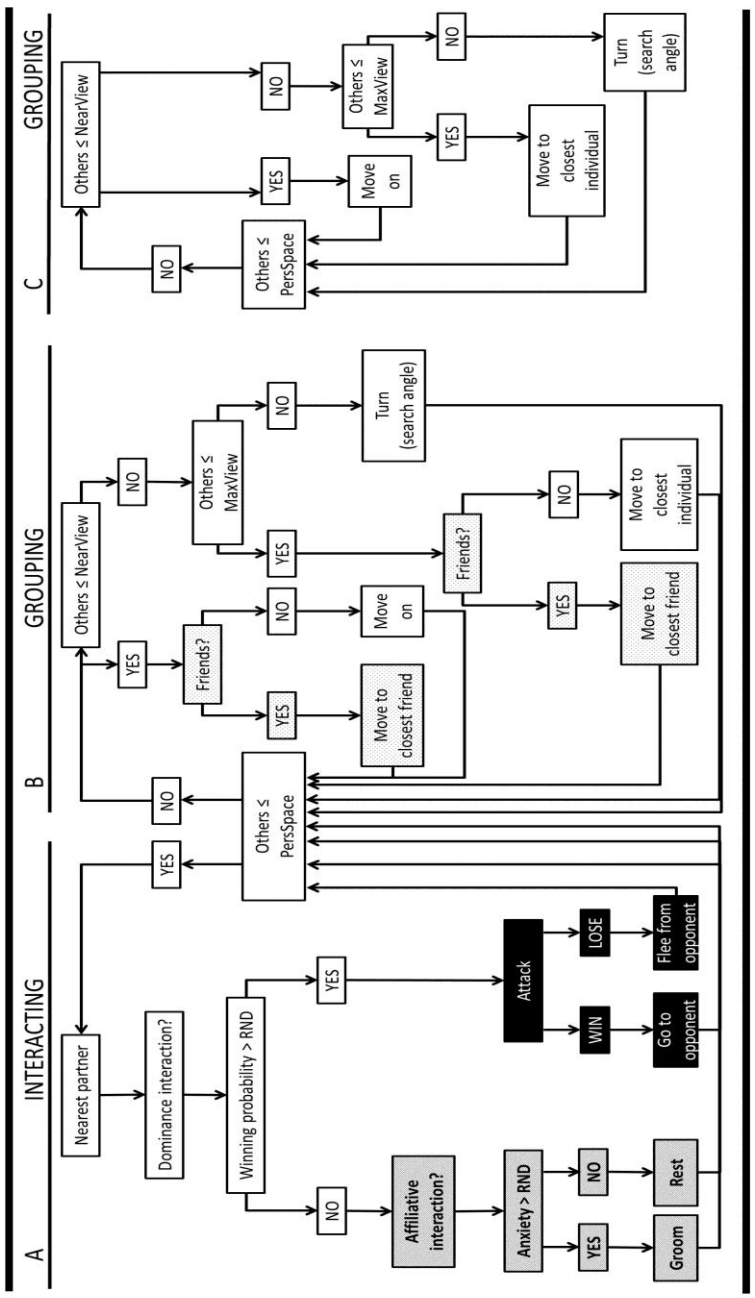

Figure 1. Rules for interacting and grouping in FriendsWorld and GrooFiWorld.
A. The interaction rules are the same for both models: solid black boxes show the dominance interactions and grey boxes the affiliation interactions.
B. Grouping rules in FriendsWorld, the white dotted boxes show the friends rules in *NearView* and *MaxView*. **C.** Grouping rules in GrooFiWorld.

Expected outcomes have a lower impact, high ranking individuals will increase their *Dom* value slightly after winning a fight; however, an unexpected victory from a low ranking individual will lead to a greater increase in its relative *Dom* value. In order to keep *Dom* values positive, their minimum is set to 0.01. The change in dominance values (*Dom*) is multiplied by a scaling factor between 0 and 1, called *StepDom* (Table 1), a high *StepDom* value indicates fierce aggression, and a low *StepDom* value indicates mild aggression (Hemelrijk 1999a). After a fight, the winner chases the loser over a distance of one unit (*ChaseDist*, Table 1), and then it turns randomly 45 degrees to the left or the right. The loser reacts by fleeing over a fixed distance of 2 units (*FleeingDist*; Table 1), and then it turns randomly 45 degrees to the left or right. The turning angle prevents repeated interactions between same partners after a fight.

Grooming rules

In real primates, grooming is influenced by several physiological conditions, such as stress levels (Sapolsky 1992) and opiate concentrations (Keverne et al. 1989; Graves et al. 2002). These physiological mechanisms are reflected in the model by an anxiety value which ranges from 0 to 1, with 0 being relaxed and 1 being very tense. When an individual decides not to fight, it will consider whether to groom its partner or not, depending on its anxiety value. If its anxiety value is higher than a random number between 0 and 1, the individual will groom its partner; otherwise, it does nothing (Fig 1A). To prevent repeated interactions between the same partners, after grooming both partners turn randomly to the left or right over an angle of 45 degrees.

In line with empirical studies, grooming reduces anxiety in both individuals; it does so more in the groomee (*AnxDcrGree*), than in the groomer (*AnxDcrGrmr*) (Table 1); if individuals do not groom for a certain amount of time, their anxiety level increases (*AnxInc*, Table 1) (Keverne et al. 1989; Graves et al. 2002). Since, in empirical studies it has been shown that former opponents increase their anxiety after a fight (Aureli et al. 2002), in the model anxiety also increases in both opponents after a fight by *AnxIncFight* (Table 1).

Parameters and experimental set-up

Parameter values are the same as in previous versions of the GrooFiWorld model except group size which was increased from 12 to 16 individuals (Puga-Gonzalez et al. 2009). This increment in Group size was done in order to increase statistical power and thus point out differences between GrooFiWorld and FriendsWorld. Following empirical studies, sex ratios were biased towards females: at high intensity of aggression (intolerant societies) groups comprised 80% females, and at low intensity (tolerant societies) 70% (Caldecott 1986; Ménard 2004). To reflect sexual dimorphism, initial dominance values, *InitDom,* were set at 16 for females and 32 for males (Table 1).

Data collection and analysis

Simulations were run at high and low intensity of aggression. Each simulation consists of 10 separate runs divided into 260 periods. Each period consists of 320 activations (i.e. GroupSize, 16*20). To avoid transient dominance values, data are collected from period 200 to 260 (Hemelrijk 1999a; Puga-Gonzalez et al. 2009). Data recorded include the individual's spatial position and its social interactions. During social interactions, we recorded the identities of the winner and loser of a fight and their *Dom* values, as well as the identities of groomer and groomee and their anxiety values. Results are presented as the average of the ten runs, with their combined probability using the improved Bonferroni procedure (Hochberg 1988). To test for differences between high and low intensity of aggression and between GrooFiWorld and FriendsWorld, we use Mann Whitney U tests. P-values are two-tailed except when the result is expected to differ in a specific direction.

The percentage of time females spent fighting (or grooming) is measured as the total number of fights (or grooming bouts) in the group divided by total number of activations (Puga-Gonzalez et al. 2009). The steepness of the hierarchy is calculated by obtaining the coefficient of variation of the *Dom* values. For each run, the average value over periods 200-260 is calculated and averaged over the 10 runs. The higher the coefficient of variation, the steeper the hierarchy, indicating that differences between ranks are very pronounced (Hemelrijk 1999a). Ranks are

calculated by averaging the *Dom* values of each individual over periods 200-260. Centrality of individuals is calculated by using circular statistics (Hemelrijk 1999a): a circle is drawn around ego and the direction of the other group members are projected as points on the circumference (Mardia 1972). This measurement returns several vectors. The length of the average vector then represents the amount of clustering found within the group. A long average vector indicates that an individual is found at the periphery of the group. Hence, centrality of dominants is represented by a negative correlation between rank and the length of average vector.

Reconciliation between former opponents is measured via the improved PC-MC method (Post-Conflict versus Matched-Control) (Veenema et al. 1994), which compares the time at which grooming occurs shortly after a conflict, the Post-Conflict period, and the moment grooming occurs in a control period of the same length, the Matched-Control, recorded a day later during the same time. Here, we use the PC-MC method as described in Puga-Gonzalez et al. (2009). Conciliatory tendency is defined in equation 3.

$$ConciliatoryTendency = \frac{AttractedPairs - DispersedPairs}{TotalNumberOfPairs} \qquad \textit{Eq. (3)}$$

We used matrix Tau-Kr correlations to test for the distribution of social interactions: grooming, aggression and reconciliation (Hemelrijk 1990a). The level of significance was calculated using 2000 permutations. Reciprocation of grooming and aggression are tested by correlating an actor and a receiver's matrix. Positive correlations indicate reciprocity and negative correlations indicate uni-directionality (Hemelrijk 1990a). Whether grooming is directed up the dominance hierarchy or towards individuals of similar rank is measured by correlating the matrix of grooming given with a partner-rank matrix and a similar-rank matrix respectively. The partner-rank matrix is filled with the average *Dom* values of each partner in the rows. The similar-rank matrix is filled with zeros apart from the

partners closest and second closest in rank, which are indicated as 1's. Since higher-ranking individuals have higher *Dom* values, a significantly positive correlation with the partner-rank matrix means that grooming is directed up the dominance hierarchy, while a positive correlation with the similar-rank matrix corresponds to grooming directed towards individuals of similar ranks (Hemelrijk 1990a).

The diversity of interaction partners was measured to test whether individuals in FriendsWorld were more selective in their interaction partners than in GrooFiWorld. Two different diversity indices are used: Berger-Parker dominance index (Southwood 1978) and the percentage of non-interacting dyads. In addition, we also measured the stability of friends during the whole simulation.

The Berger-Parker dominance index is calculated by dividing the frequency of grooming of ego with its favourite partner (i.e. the individual with whom it has the highest number of interactions) by the total grooming frequency of ego with all other individuals (equation 4) (Southwood 1978; Hemelrijk & de Kogel 1989). The higher the Berger-Parker dominance index, the less diverse the interacting partners.

$$BP = \frac{Groo\min gFrequencyBetweenIndivdualsA\&B}{TotalGroo\min gFrequencyOfIndividualA} \qquad \textit{Eq. (4)}$$

To calculate the relative number of non-interacting dyads we count the number of dyads that never interacted and divided it by the total number of possible dyads (i.e. 120). To analyse the stability of friendships, every 20 periods (from period 200 to 260) we recorded, per individual, the percentage of friends that remain the same. Results are based on the average percentage of the group per run.

Results

Dominance style and affiliative patterns

In FriendsWorld similar patterns emerge regarding dominance and affiliation and their differences between high and low intensity of aggression (Table 2). In contrast to low intensity of aggression, at high intensity: the gradient of the hierarchy is

steeper (1 in Tables 2 & 3B), females are more dominant over males (2 in Tables 2 & 3B), aggression is unidirectional rather than bidirectional (3 in Tables 2 & 3B), centrality of dominants is stronger (4 in Tables 2 & 3B), time spent fighting is lower (5 in Tables 2 & 3B), groups are less cohesive (6 in Tables 2 & 3B), time spent grooming is lower (7 in Tables 2 & 3B), the percentage of coalitions is higher (8 in Tables 2 & 3B), reconciliation is less frequent (9 in Tables 2 & 3B), grooming is directed up the dominance hierarchy and occurs more frequently among partners of similar rank (10-11 in Tables 2 & 3B), and individuals reconcile more often with valuable partners (12 in Tables 2 & 3B).

	High intensity of Aggression		**Low intensity of Aggression**	
	GrooFiWorld	**FriendsWorld**	**GrooFiWorld**	**FriendsWorld**
DOMINANCE STYLE				
1) Gradient of the hierarchy	0.82	0.88	0.11	0.12
2) Female dominance	0.29	0.31	0	0
3) Unidirectionality of aggression	-0.35**	-0.02**	0.40**	0.48**
4) Centrality of dominants (Tau)	-0.48**	-0.40**	-0.08	-0.20
5) Time spent fighting %	14	18	18	24
6) Average nearest neighbour distance	4.29	3.89	3.6	2.75
AFFILIATIVE PATTERNS				
7) Time spent grooming (%)	16	19	20	25
8) Coalitions (%)	9	9	7	8
9) Conciliatory tendency (%)	18	15	30	27
10) Grooming up the hierarchy	0.41***	0.37**	0.11*	0.11*
11) Grooming among similar ranks	0.15*	0.14*	0.07	0.02
12) Reconciliation with valuable partners	0.36**	0.49**	0.04*	0.03

Table 2. Dominance style and affiliative patterns in GrooFiWorld and FriendsWorld.

Results are average of ten runs. * p<0.05; **p<0.01; ***p<0.001.

Comparing FriendsWorld to GrooFiWorld, the patterns of dominance style and affiliation differ mostly at low but not at high intensity of aggression (Table 3 C&D). At high intensity of aggression only 1 out of 12 patterns differ: in FriendsWorld, individuals spent significantly more time fighting than in GrooFiWorld (5 in Tables 2 & 3C). At low intensity of aggression 5 out of 12 patterns differ: in FriendsWorld individuals 1) spend more time fighting (5 in Tables 2 & 3D), 2) are closer to their neighbours (6 in Tables 2 & 3D), 3) spent more time grooming (7 in Tables 2 & 3D), 4) form coalitions more frequently (8 in Tables 2 & 3D), and 5) reconcile less frequently (9 in Tables 2 & 3D) than in GrooFiWorld.

	GrooFiWorld	**FriendsWorld**	**GrooFiWorld vs FriendsWorld**	
	A) High vs low	**B) High vs Low**	**C) High**	**D) Low**
DOMINANCE STYLE				
1) Gradient of the hierarchy	U = 100 ***	U = 100 ***	U = 61 NS	U = 63 NS
2) Female dominance	U = 95 ***	U = 100 ***	U = 53 NS	U = 50 NS
3) Unidirectionality of aggression	U = 100 ***	U = 84 **	U = 72 NS	U = 74 NS
4) Centrality of dominants (Tau)	U = 92 **	U= 78 *	U = 57 NS	U= 53 NS
5) Time spent fighting %	U = 100 ***	U = 100 ***	U = 100 ***	U = 100 ***
6) Average nearest neighbour distance	U = 98 ***	U = 100 ***	U = 73 NS	U= 100 ***
AFFILIATIVE PATTERNS				
7) Time spent grooming (%)	U = 100 ***	U = 97 ***	U = 76 NS	U = 100 ***
8) Coalitions (%)	U = 96 ***	U = 70 NS	U = 52 NS	U = 95 ***
9) Conciliatory tendency	U = 100 ***	U = 100 ***	U = 68 NS	U = 82 *
10) Grooming up the hierarchy	U = 100 ***	U = 95 ***	U = 57 NS	U = 52 NS
11) Grooming among similar ranks	U = 72 NS	U = 79 *	U = 46 NS	U = 61 NS
12) Reconciliation with valuable partners	U = 98 ***	U = 100 ***	U = 71 NS	U = 53 NS

Table 3. Comparison of dominance and affiliative patterns. Between high and low intensity of aggression in **A)** GrooFiWorld and **B)** FriendsWorld; and between FriendsWorld and GrooFiWorld at **C)** high and **D)** low intensity of aggression. Mann-Whitney U test: two-tailed p-values of tests are combined via the improved Bonferroni method. NS, not significant; * p<0.05; **p<0.01; ***p<0.001.

Reciprocation and interchange of grooming and support

Patterns of reciprocation and interchange of grooming and support also emerge in the FriendsWorld model and, except for reciprocation of grooming, all of them are significantly stronger at high than at low intensity of aggression (2-4 in Tables 4 & 5B). Comparing GrooFiWorld to FriendsWorld, in FriendsWorld at high intensity of aggression 3 out of 4 patterns of reciprocity and interchange are significantly stronger: 1) reciprocity of support, 2) support received for grooming given, and support given for grooming received (2-4 in Tables 4 & 5C).

	High intensity of Aggression		**Low intensity of Aggression**	
	GrooFiWorld	**FriendsWorld**	**GrooFiWorld**	**FriendsWorld**
1) Grooming Reciprocation	0.37***	0.51**	0.45***	0.50***
2) Reciprocity of support	0.35**	0.50**	0.19**	0.23**
3) Support received for grooming given	0.41***	0.55***	0.25**	0.22**
4) Support given for grooming received	0.26**	0.44**	0.30**	0.29**

Table 4. Reciprocation and interchange of grooming and support in GrooFiWorld and FriendsWorld. TauKr matrix correlations, results are average of ten runs.

Interactions among Friends in GrooFiWorld and FriendsWorld

In FriendsWorld at high intensity of aggression, individuals were more selective with their interaction partners: the percentage of non-interacting dyads and the Berger-Parker dominance index were higher than in GrooFiWorld (1-3, in Tables 6 & 7C). Besides, in FriendsWorld individuals maintain usually the same friends during the whole simulation, whereas in GrooFiWorld individuals change friends more frequently (4 in Tables 6, 7C & 7D).

In both models, individuals attack and support friends significantly more than non-friends (Table 8, 9 A & B). Besides, in FriendsWorld at high intensity of aggression friends attack and support each other more often than friends in GrooFiWorld; this was not the case for low intensity of aggression (Table 8, 9C).

	GrooFiWorld	FriendsWorld	GrooFiWorld vs FriendsWorld	
	A) High vs low	B) High vs Low	C) High	D) Low
1) Grooming Reciprocation	U = 77 *	U = 57 NS	U = 69 NS	U =69 NS
2) Reciprocity of Support	U = 85 **	U = 94***	U = 77*	U = 71 NS
3) Support received for grooming given	U = 92 ***	U = 100***	U = 79*	U = 64 NS
4) Support given for grooming received	U = 66 NS	U = 77*	U = 76*	U = 50 NS

Table 5. Comparison of TauKr coefficient values of reciprocation and interchange. Between high and low intensity of aggression in **A)** GrooFiWorld and **B)** FriendsWorld, and between FriendsWorld and GrooFiWorld at **C)** high and **D)** low intensity of aggression. Mann-Whitney U test: one-tailed p-values are combined via the improved Bonferroni method. NS, not significant;* p<0.05; **p<0.01; ***p<0.001.

Discussion

In FriendsWorld, all of the patterns of dominance style, affiliation, reciprocation and interchange of grooming and support and their respective differences between high and low emerge (Table 2 and 3). The addition of social bonding, however, had a quantitative effect on the patterns of reciprocation and interchange at high intensity of aggression. In FriendsWorld, these patterns became significantly stronger than in GrooFiWorld (Tables 4 and 5C). Thus, it seems that the mere act of keeping proximity to friends is sufficient to reinforce reciprocation and interchange of social acts.

	High intensity of Aggression		Low intensity of Aggression	
	GrooFiWorld	FriendsWorld	GrooFiWorld	FriendsWorld
1) Percentage of non-interacting dyads	2	18	0	0
2) Berger-Parker Dominance index (one top groomer)	0.19	0.26	0.17	0.16
3) Berger-Parker Dominance index (three top groomers)	0.44	0.57	0.42	0.43
4) Stability of friends (%)	37	51	28	32

Table 6. Diversity of partners and stability of friends in GrooFiWorld and FriendsWorld.

Results are average of ten runs.

	GrooFiWorld	FriendsWorld	GrooFiWorld vs FriendsWorld	
	A) High vs low	**B) High vs Low**	**C) High**	**D) Low**
1) Percentage of non-interacting dyads	U = 55 NS	U = 70 *	U = 66 NS	U = 50 NS
2) Berger-Parker Dominance index (one top groomer)	U = 61 NS	U = 89 **	U = 72 *	U = 71 NS
3) Berger-Parker Dominance index (three top groomer)	U = 53 NS	U = 83 **	U = 73 *	U = 70 NS
4) Stability of friends	U = 694 ***	U = 736.5 ***	U = 634.5 **	U = 612.5 *

Table 7. Comparison of the values of diversity of partners and stability of friends. Comparison between high and low intensity of aggression in **A)** GrooFiWorld and **B)** FriendsWorld; and between FriendsWorld and GrooFiWorld at **C)** high and **D)** low intensity of aggression. Mann-Whitney U test: two-tailed p-values are combined via the improved Bonferroni method. NS, not significant; * p<0.05; **p<0.01; ***p<0.001.

The stronger reciprocation and interchange of grooming and support at high intensity of aggression in FriendsWorld was due to the more frequent interactions of individuals with their friends than with non-friends (Table 8 and 9C). This is supported by the fact that individuals in FriendsWorld, i) are more selective in their interaction partners (2-3 in Table 6), and ii) keep the same friends over a longer time period (4 in Table 6) than in GrooFiWorld. Thus, the tendency of individuals to move towards their friends causes individuals to be often in the proximity of their friends and as a consequence interact most often with them.

In contrast to high intensity of aggression, at low intensity reciprocation and interchange did not become stronger in FriendsWorld than in GrooFiWorld. This was probably due to the fact that at low intensity of aggression friends in FriendsWorld interact as frequent as in GrooFiWorld (Table 8 and 9C). A combination of factors may account for this result. In both models, GrooFiWorld and FriendsWorld, at low intensity of aggression there is no correlation between dominant individuals and centrality which means that the spatial structure of the group is less rigid than at high intensity of aggression (4 in Table 3). Individuals, therefore, may interact equally often with everybody. In addition, because of the

shallow dominance hierarchy, individuals experience more or less the same risk when interacting with a dominant or a subordinate individual and as a result they may distribute their grooming equally among all group members. This may cause individuals to change friends frequently. Since friends change as frequently as in GrooFiWorld, reciprocation and interchange remain the same also.

In FriendsWorld, social bonding is represented cognitively even simpler than emotional bookkeeping. Individuals develop friendships through repeated grooming interactions and try to keep proximity to their most frequent grooming partners. In contrast to what is suggested by emotional bookkeeping, individuals in FriendsWorld do not intent to reciprocate or interchange grooming and support more with friends than with non-friends. Thus, the results of the model show that an intention to reciprocate or interchange may not be necessary for these patterns to emerge. What really matters is to have differentiated proximity relationships, i.e. tend to be closer to some than with others, and consequently, reciprocation and interchange emerge automatically.

	High intensity of aggression				**Low intensity of aggression**			
	GrooFiWorld		**FriendsWorld**		**GrooFiWorld**		**FriendsWorld**	
	Friends	Non-Friends	Friends	Non-Friends	Friends	Non-Friends	Friends	Non-Friends
Time spent attacking (%)	62	38	73	27	63	37	63	37
Time spent supporting (%)	68	32	76	24	63	37	62	38

Table 8. Interaction frequencies between friends and non-friends in GrooFiWorld and FriendsWorld. Results are average of ten runs.

	Intensity of aggression	
	High	**Low**
A) GrooFiWorld (friends vs non-friends)		
Time spent attacking (%)	U = 100 ***	U = 100 ***
Time spent supporting (%)	U = 100 ***	U = 100 ***
B) FriendsWorld (friends vs non-friends)		
Time spent attacking (%)	U = 100 ***	U = 100 ***
Time spent supporting (%)	U = 100 ***	U = 100 ***
C) GrooFiWorld vs FriendsWorld (friends vs friends)		
Time spent attacking (%)	U = 100 ***	U = 52 NS
Time spent supporting (%)	U = 100 ***	U = 50 NS

Table 9. Comparison of interaction frequencies. Comparison between friends and non-friends at high and low intensity of aggression in **A)** GrooFiWorld, **B)** FriendsWorld, and **C)** between friends in FriendsWorld and friends in GrooFiWorld. Mann-Whitney U test: two-tailed p-values are combined via the improved Bonferroni method. NS, not significant; * p<0.05; **p<0.01; ***p<0.001.

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Chapter 7

Discussion

Reconciliation with the time-rule method

In empirical research, reconciliation is usually confirmed with two different methods, the MC-PC method (Veenema et al. 1994) and the time-rule method (Aureli et al. 1989). In chapter 2, I demonstrated the occurrence of reconciliation with the MC-PC method. Here, I will briefly show that in the model reconciliation is also demonstrated with the time-rule method.

The time rule method relies on the fact that the frequency of affiliative contacts between former opponents is usually high early in the post-conflict period (PC), whereas the frequency of affiliative contacts in the control period (MC) is more evenly distributed through time. In other words, the method compares the frequency of affiliative contacts at different points in time during the PC and MC periods. Reconciliation is then defined as the affiliative contact that occurs during the time interval in which the frequency of affiliative contacts during the PC is higher than in the MC. To analyse reconciliation with the time-rule method in the model, the PC and MC periods had to be extended from three to five activations. This is necessary because during the first three activations after the conflict the frequency of affiliative contacts during the PC was still higher than in the MC (Fig 1). Results show that at both high and low intensity of aggression, reconciliation occurs during the first three activations after the conflict (Fig 1). Further, when there is no spatial structure, reconciliation does not occur (Fig 1). This corroborates that in the model reconciliation occurs as a side-effect of proximity.

Controlling for proximity during the control period in analysis of reconciliation

In chapter 2 I showed that in the model, the most likely mechanism behind the emergence of reconciliation was proximity because reconciliation disappeared without the spatial structure of the group. If this is indeed true, reconciliation should also disappear when proximity between former opponents is controlled during the MC period. This was indeed the case, as the distance of proximity between former opponents decreases during the MC period, the conciliatory tendency also decreases (Table 1). This result, thus, corroborates the assumption

that in the model reconciliation is a side-effect of closer proximity between former opponents during the post-conflict period than otherwise. This is in line with empirical studies showing that conciliatory tendency decreases, although it does not disappear, when controlling for proximity during the MC (Matsumura 1996; Petit et al. 1997; Swedell 1997; Call 1999; Call et al. 1999; Kutsukake & Castles 2001; Majolo et al. 2005; Majolo & Koyama 2006; Cooper et al. 2007). As shown by the model, whether conciliatory tendency disappears or not may depend on the distance of proximity controlled for (Table 1). Thus, in these empirical studies it may be that the distance of proximity controlled for was not appropriated and thus the conciliatory tendency was only reduced.

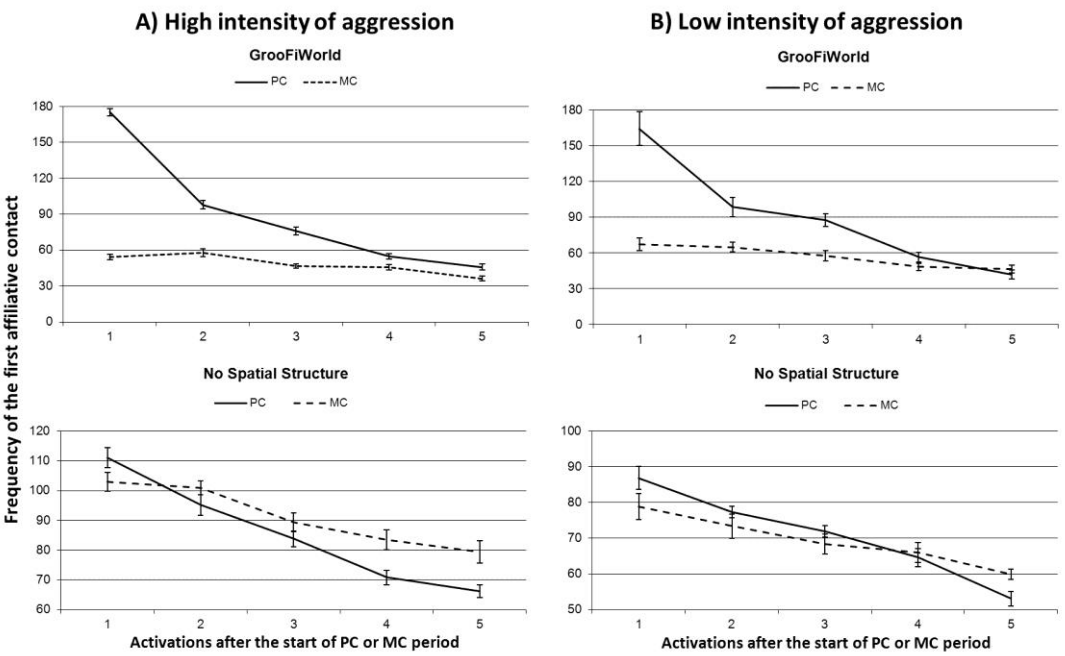

Fig 1. Reconciliation measured with the Time-rule method. The graphs show the frequency of the first affiliative contact between former opponents in the PC and MC period at A) high and B) low intensity of aggression in the GrooFiWorld model and in the model without spatial structure. Results are average of 10 runs ± SE.

	Distance between former opponents in MC			
	No control	10 units	7.5 units	5 units
High intensity of aggression	16%	5%	**-9%**	**-28%**
Low intensity of aggression	21%	15%	6%	**-6%**

Table 1. Conciliatory tendency at high and low intensity of aggression in GrooFiWorld when controlling for different units of spatial distance between former opponents during the MC. Results are average of 10 runs. In bold negative tendencies.

GrooFiWorld with coalition rules

In the GrooFiWorld model, the formation of coalitions was incidentally. This means that individuals lacked an intention to support others in fights, a point of view that may not be shared by some empirical researchers. Therefore, in a separate study, we investigated what happens if individuals have an intention and a preference to support one individual rather than the other (Sarkol et al. 2009). In this study and in further analysis we showed that reciprocation and interchange of grooming and support still emerge in the model. Three different rules on whom to support were tested in the model: (i) “support the higher ranking”, (ii) “support the one from whom you have received the most grooming” and (iii) “support one at random”. Coalitions were implemented as follows. At the start of a fight a potential supporter was selected from within a predefined space, Coalition Space (*CoaSpace*), i.e. a circumference around each of the combatants (fig 2). *CoaSpace* was greater than *PerSpace* but smaller than NearView, its radius was set to 10 units. If no individual was within *CoaSpace*, the dyadic fight continued. If more than one individual were within *CoaSpace*, the one with the closest distance to one of the combatants was chosen as potential supporter (fig 2).

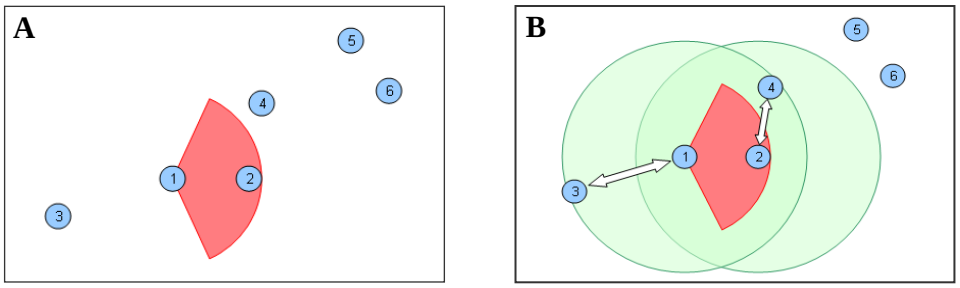

Figure 2. Selection of a potential supporter in GrooFiWorld with coalition rules. In panel **A** two individuals fight: individual 2 (within *PerSpace* of individual 1) is being attacked by individual 1. In panel **B** is shown the combined *CoaSpaces* of individuals 1 and 2; from within this zone other individuals may be selected as potential supporters. Individual 3 and 4 are both in *CoaSpace* and therefore are potential supporters. Since individual 4 is the closest to one of the opponents (individual 2), it is selected as potential supporter. Individuals 5 and 6 are not affected by the fight.

Once a potential supporter was selected, it would choose which of the two combatants to support following one of the rules mentioned above (this rule was predefined at the start of the simulation, thus individuals could not actively choose a supporting rule). After choosing the recipient of support, the supporter assessed the risk of fighting the target of the coalition as if it were fighting alone (see dominance interactions in chapter 3). If the supporter thought it was too risky to fight, it would do nothing and the dyadic fight would continue, but if the supporter decided to attack, a coalition would happen. The outcome of the coalition was determined by the combined strengths of all three individuals. Results show that no matter what coalition rule individuals used, patterns of reciprocation and interchange still emerged in the model (Table 2). This was surprising because I expected to find differences between coalition rules. A probable explanation for this result is given by the fact that before joining a coalition a potential supporter first assesses the risks of fighting the potential target alone as in a dyadic fight. This may preclude the emergence of differences because, no matter the rule, a potential supporter may never join a coalition if the potential target was higher ranking than it. Nevertheless, these results show, as in chapter 3, that in this

version of the model the socio-spatial structure of individuals is also the main driver of reciprocity and interchange because without it these patterns become significantly weaker -at high intensity of aggression- or disappear -at low intensity- (results not shown). This suggests that also in real primates spatial constraints may overrule strategic considerations.

	Support:					
	Highest ranking		**From whom you received most grooming**		**At random**	
Intensity of aggression	High	Low	High	Low	High	Low
Reciprocation of support	0.38***	0.20***	0.28***	0.32***	0.17***	0.21***
Grooming for support	0.42***	0.27***	0.40***	0.36***	0.36***	0.32***
Support for grooming	0.34***	0.26***	0.36***	0.41**	0.31***	0.38***

Table 2. TauKr correlations for reciprocity and interchange of grooming and support in GrooFiWorld with three different rules for support. Results are average of 10 runs, Bonferroni corrected. *p<0.05; **p<0.001; ***p<0.001.

GrooFiWorld in an evolutionary context

Recently, theoretical studies on the evolution of reciprocation have shown that for reciprocity to arise individuals must have differentiated relationships (Hamilton & Taborsky 2005; Rankin & Taborsky 2009; Barta et al. 2011; van Doorn & Taborsky 2012). These studies, however, do not suggest how differentiated relationships may emerge in the first place. The GrooFiWorld model offers a mechanism for the emergence of differentiated relationships, i.e. by means of the spatial structure of individuals in the group and the self-reinforcing effects of dominance. In GrooFiWorld, a socio-spatial structure emerges because dominant individuals are fearless (sense low risk of losing fights) and thus, are free to move wherever they want by chasing low ranking individuals. Consequently, dominant individuals are usually in the center of the group whereas low ranking ones are in the periphery. This spatial structure causes that some individuals interact more with some than with others and thus reciprocation and interchange emerge automatically. How

rigid is this spatial structure depends on intensity of aggression and cohesiveness of the group (Hemelrijk 1999b). When intensity of aggression is high, the spatial structure is more rigid than at low intensity and thus, relationships are more differentiated (chapters 2, 3 and 6).

A main critique to this study is the lack of evolution in the model. However, the main aim of our model was to highlight proximate mechanisms of social complexity and develop new hypotheses that may be hindered when thinking in a purely adaptive framework. In the macaque system, several socio-behavioural traits seem to exist as an integrated package and to co-vary together, i.e. a change in one trait may cause a change in all the others. Thus, it is important to identify first which of these traits may be under selection pressure and which ones may be a side-effect or a consequence thereof, instead of assuming an adaptive history for every single trait. As shown in this thesis, intensity of aggression is crucial for the development of the socio-spatial structure of the group which in turn causes the emergence of many other socio-behavioural patterns. Moreover, whether the patterns that emerge resemble despotic or egalitarian societies depend on cohesiveness of the group and on whether intensity of aggression is high or low (Hemelrijk 1999b). Hence, the model suggests intensity of aggression as a possible candidate trait which may have been under selection pressure (Hemelrijk 2002a). Interestingly, although the three main socio-ecological models suggest different ecological factors (e.g. food distribution, population density, predation risks, infanticide) as probable causes of despotic or egalitarian dominant styles, they agree on one factor; namely, that the distribution of resources may determine the strength of feeding competition (Sterck et al. 1997; Isbell & Young 2002). Thus, the distribution of resources could have selected for intensity of aggression which in turn may determine the socio-spatial structure of the group and, as a side-effect, several other behavioural traits emerge (Hemelrijk 2002a). When resources are clumped and can be monopolized competition may often involve overt agonistic interactions which may select for fierce aggression. However, when resources are evenly distributed and cannot be monopolized overt agonistic interactions may be rare and thus mild aggression may be evolutionary favored. In addition,

competition for resources also creates tension among group members, and thus natural selection may have favoured the use of grooming as a mechanism to alleviate this tension. In GrooFiWorld social interactions are based on these two basic features, aggression and grooming as a tension reduction mechanism. As such, the model may represent the complex social behaviour emerging once primates started living in groups. Whether during the course of evolution natural selection may have favoured the use of sophisticated cognition in the display of some behaviour is possible. However, to determine whether sophisticated cognition is involved or not it is necessary to exclude first the possibility of simpler mechanisms such as those suggested by GrooFiWorld.

In sum, socio-ecological models suggest that group living in primates may have evolved as protection against predators and infanticide (van Schaik 1989; Sterck et al. 1997; Isbell & Young 2002). However, group living creates competition for resources which depending on their distribution may have driven the evolution of fierce or mild aggression. Intensity of aggression and cohesiveness of the group determine the spatial structure and as a side-effect the emergence of many other socio-behavioural patterns. Once this network of socio-behavioural traits emerged, natural selection may have favoured the use of sophisticated cognition on some patterns. Thus, it would be now interesting to integrate this system with an evolutionary approach, i.e. what may happen if some behaviours are favoured more than others.

English summary

This thesis started by extending a previous model of grouping and aggression, the DomWorld model. The extension consisted on the addition of grooming behaviour. I showed that by extending the model with a single, cognitively simple rule on when to groom others, all commonly acknowledged patterns of affiliation and aggression in primates (particularly macaques) emerged. Further, by changing intensity of aggression from low to high, the affiliative and aggressive patterns switched from those resembling egalitarian to those resembling despotic societies. The results of the model suggest that the specific cognitive processes thought to underlie post-conflict affiliations, reciprocation, and interchange of grooming and support, may not be necessary. Although the model cannot refute the use of sophisticated cognitive processes, it shows how a simple, parsimonious mechanism, mainly simple rules of thumb in combination with the spatial positioning of individuals in the group, may result in many complex socio-behavioural patterns which may seem to be the product of intelligent behaviour.

The main part of this thesis started in **Chapter 2** where I explored the consequences of adding grooming behaviour to the Dom-World model. In the new model called GrooFiWorld (Grooming and Fighting world), I looked at the distribution of grooming among individuals and their differences between high and low intensity of aggression. I validated the model by comparing the affiliative patterns that emerged with those described in empirical data of despotic and egalitarian societies of macaques. The model provided us with new explanations as regards reciprocation of grooming, grooming directed up the dominance hierarchy and towards individuals of similar rank. Further, in this chapter I also studied the emergence of post-conflict affiliation between former opponents, i.e. reconciliation, in the model. The emergence of reconciliation was unexpected since in the model individuals have neither memory of the former opponent nor a conciliatory disposition, traits thought necessary for individuals to reconcile (de Waal & Yoshihara 1983). Reconciliation was due to the closer proximity of former opponents after the fight than otherwise which indicates the necessity of

controlling for proximity in empirical studies of reconciliation. Moreover, at high intensity of aggression reconciliation occurred more frequently between valuable partners, i.e. between individuals that groom most frequently. This was remarkable because to reconcile with valuable partners it is thought that individuals need to assess and compare past and future interactions. In the model, however, this happens because due to the spatial positioning of individuals in the group, individuals interact more with some than with others.

Surprisingly, in the model we observed coalitions when incidentally, after a fight between two individuals (A and B), a third individual (C) attacked one of the two combatants (e.g. A). Here, C supported B and opposed A. Thus, in **chapter 3** I studied the formation of coalitions and coalition patterns. Coalition patterns are considered to show most clearly the sophisticated cognition of primates because they are thought to reveal, 'triadic awareness', 'calculated reciprocity' and even 'revenge'. In this chapter, however, the results of the model showed that calculated reciprocity may not be necessary for reciprocation and interchange of grooming and support. Instead, differentiated relationships are sufficient for these patterns to arise. In the model, differentiated relationships emerge as a consequence of the socio-spatial structure of the group which causes individuals to interact more frequently with some than with others and thus, the emergence of reciprocation and interchange of grooming and support. This was further corroborated in **chapter 6** when the model was extended to investigate the effects of 'friendships' on the patterns of reciprocation and interchange of grooming and support. In the new model called 'FriendsWorld', individuals explicitly seek to stay close to their 'friends', those with whom they affiliate the most. This reinforced the differentiation of relationships because individuals interacted more with their friends than with non-friends. As a consequence, the patterns of reciprocation and interchange of grooming and support became significantly stronger in FriendsWorld than in GrooFiWorld. Importantly, individuals do not interact differently with friends than with non-friends. Hence, it is not that individuals intent to reciprocate and interchange more with friends than with non-friends

what causes the strengthening of the patterns; rather, it is the more frequently interactions between friends.

In **chapter 4**, I tested in three species of macaques the predictions delivered by the model in **chapter 3** regarding patterns of grooming and opposition in fights. These predictions suggested, among other things, that individuals groom others for the receipt of opposition which is counterintuitive if one assumes that individuals intentionally reciprocate and interchange services. Thus, testing these predictions was important because if found in empirical data, it would be an indication that the mechanism suggested by the model may be indeed occurring in real primates. The predictions were supported by the empirical data, female macaques: A) attacked more often those whom they usually opposed in a coalition and received more often opposition from those from whom they usually received more frequent attacks; and B) groomed more often those from whom they usually received opposition in a coalition and opposed more often those from whom they received more often grooming. Because in the model these patterns are a consequence of the spatial structure, their confirmation in empirical data supports the suggestion that in real primates coalition patterns may also be a consequence of the spatial structure of the group.

In chapter 5 I investigated the occurrence of post-conflict affiliation between bystanders and former opponents of a fight in an empirical study of tonkean macaques, *Macaca tonkeana,* and in the model. Here, for the first time I used the model to successfully mimic a group of real monkeys. The results showed that patterns of post-conflict affiliation were similar in both the model and empirical data. The model suggested two different mechanisms for the emergence of post-conflict affiliation with bystanders: anxiety reduction and social facilitation. Social facilitation was responsible for the emergence of post-conflict affiliation received from bystanders. In the model, social facilitation increases the chances of bystanders being activated next after the fight. In real animals then, a fight between two or more individuals may increase the arousal of bystanders and thus, the likelihood of interacting with former combatants after the conflict is over. Reduction of anxiety was the main driver of solicitation of post-conflict affiliation.

Because a fight is a stressful event, combatants are anxious after the conflict is over, a fact corroborated in empirical studies and implemented in the model. Thus, after the termination of the conflict former combatants may try to relieve their anxiety by grooming a bystander. The mechanisms suggested by the model are more parsimonious than the ones currently proposed (e.g. cognitive empathy) and thus, they deserved to be investigated empirically more thoroughly.

Overall, the model GrooFiWorld proposes an integrative theory of affiliative and aggressive behaviour of primates. The key trait is intensity of aggression. Intensity of aggression determines the steepness of the hierarchy and the spatial position of individuals in the group. When intensity of aggression is high, the patterns that emerge resemble those found in intolerant societies: the dominance hierarchy is steep; individuals direct grooming up the dominance hierarchy and towards individuals of similar rank; aggression and contra-support are unidirectional; conciliatory tendency, time spent grooming and fighting are low; and female dominance over males is high. These patterns are reverse when intensity of aggression is low. Further, the spatial positioning of individuals in the group produces differentiated relationships which are responsible for the emergence of reciprocation of grooming and support, exchange of grooming for support and support for grooming, reconciliation, and reconciliation with valuable partners. Remarkably, all these behavioural patterns emerge without assuming sophisticated cognition. Thus, the results obtained in this thesis indicate that the model GrooFiWorld captures at least some essential traits of real primate societies. Hopefully, these findings will inspire empirical researchers to investigate further the mechanisms suggested by the model.

Nederlandse samenvatting

Dit proefschrift begon ermee een vorig model uit te breiden dat groeperen en agressie betrof, het DomWorld Model. De uitbreiding behelst het toevoegen van vlooigedrag. Ik heb aangetoond dat door het model uit te breiden met één cognitief eenvoudige regel betreffende het vlooigedrag, alle bekende patronen van affiliatie en agressie in primaten (voornamelijk makaken) ontstaan. Verder door de intensiteit van agressie van laag naar hoog te veranderen, bleken de patronen van affiliatie en agressie te veranderen van die van egalitaire naar despotische gemeenschappen. De resultaten van dit model suggereren dat de specifieke cognitieve processen waarvan wordt gedacht dat ze aan de basis liggen voor postconflict sociaal gedrag, wederkerigheid en het uitwisselen van vlooigedrag en steun, in feite overbodig zijn. Hoewel het model het gebruik van ingewikkelde, cognitieve processen niet kan uitsluiten, toont het aan dat een eenvoudig mechanisme, bestaand uit simpele gedragsregels gecombineerd met de ruimtelijke verdeling van individuen, kan uitmonden in complex sociaal gedraging dat het gevolg lijkt te zijn van grote intelligentie.

Het belangrijkste gedeelte van dit proefschrift begint in **hoodfstuk 2**, waar ik de gevolgen heb onderzocht van het toevoegen van vlooigedrag in het Dom-World model. In dit nieuwe model, genaamd GrooFiWorld (Vlooien en Vechten wereld), heb ik gekeken naar de verspreiding van vlooigedrag onder individuen en de gevolgen van verschillen in hoge en lage intensiteit van agressie. Ik heb het model gevalideerd door de affiliatieve patronen die ontstonden in het model te vergelijken met empirische data van despotische en egalitaire gemeenschappen van makaken. Het model gaf ons nieuwe verklaringen betreffende de wederkerigheid van vlooien en vlooien gericht aan individuen met hogere of gelijke dominantie rang. Verder heb ik in dit hoofdstuk ook het ontstaan bestudeerd van postconflict affiliaties tussen voormalige tegenstanders, dit heet verzoening. Het ontstaan van verzoening in dit model was onverwachts, aangezien individuen geen herinneringen hebben aan eerdere tegenstanders noch een aanleg tot verzoening hebben, eigenschappen waarvan werd verwacht dat ze nodig waren voor

verzoening (de Waal en Yoshihara 1983). Verzoening ontstond omdat voormalige tegenstanders zich dichter bij elkaar bevinden na het gevecht dan anders, wat aantoont dat nabijheid een variabele is waarmee rekening moet worden gehouden in empirische onderzoeken naar verzoening. Daarenboven, wanneer agressie een hoge intensiteit had, vond verzoening vaker plaats tussen 'waardevolle' partners, oftewel zij die elkaar het vaakst vlooiden. Dit was opmerkelijk omdat men dacht dat om te kunnen verzoenen met waardevolle partners, een individu voorafgaande en toekomstige interacties moest kunnen inschatten en vergelijken. In het model daarentegen, ontstaat dit door de ruimtelijke ordening van individuen binnen de groep, waardoor sommige individuen vaker met elkaar interacteren dan met andere.

Verrassend genoeg hebben we in het model coalities geobserveerd wanneer toevallig, na een gevecht tussen twee individuen (A en B), een derde individu (C) een van de twee vechters aanviel (bijv. A). Hier steunt individu C dus individu B tegen individu A. In **hoofdstuk 3**, heb ik deze vorming van coalities en coalitiepartners bestudeerd. Coalitie patronen werden gedacht hoog ontwikkelde cognitie bij primaten aan te tonen omdat men geloofde dat zij 'triadisch bewustzijn', 'berekende reciprociteit' en zelfs de neiging tot 'wraak' onthullen. In dit hoofdstuk daarentegen, toonden de resultaten van het model dat berekende wederkerigheid mogelijk niet nodig is voor wederkerigheid en uitwisseling van vlooigedrag en steun. In plaats daarvan zijn gedifferentieerde relaties voldoende voor het ontstaan van deze patronen. In het model ontstaan gedifferentieerde relaties als gevolg van de sociale en ruimtelijke structuur van de groep. Dit veroorzaakt dat individuen vaker een interactie hebben met sommige individuen dan met andere. Zodoende ontstaat wederkerigheid en het uitwisselen van vlooigedrag en van steun. Dit werd verder bevestigd in **hoofdstuk 6** nadat het model was uitgebreid om het effect van vriendschappen te onderzoeken betreffende wederkerigheidspatronen en de uitwisseling van vlooien voor steun. In dit nieuwe model, 'FriendsWorld' genaamd, zijn individuen er expliciet op uit om bij hun 'vrienden' (diegene met wie ze het meest affiliëren) in de buurt te blijven. Dit versterkt de differentiatie van relaties omdat individuen vaker een interactie

hadden met vrienden dan met niet-vrienden. Het gevolg is dat de patronen van wederkerigheid en het uitwisselen van vlooien voor steun beduidend sterker waren in 'FriendsWorld' dan in 'GrooFiWorld'. Belangrijk hier is dat individuen niet anders interacteren met vrienden dan met niet-vrienden. Het versterken van de patronen is dus niet veroorzaakt doordat individuen de bedoeling hebben meer te reciproceren en uit te wisselen met vrienden dan met niet-vrienden; het ontstaat alleen maar doordat vrienden vaker met elkaar interacteren.

In **hoofdstuk 4** heb ik in drie makaaksoorten de voorspellingen van het model uit **hoofdstuk 3** betreffende de patronen van vlooien en tegenwerking in gevechten getest. De voorspellingen waren, onder andere, dat individuen andere vlooien in ruil voor het ontvangen van tegenwerking, wat tegen onze intuïtie ingaat als men aanneemt dat individuen reciproceren en diensten uitwisselen. Het testen van deze voorspellingen was dus belangrijk omdat wanneer deze ook gevonden worden in de empirische data, het een aanduiding zou zijn dat het door het model gesuggereerde mechanisme ook in echte primaten voorkomt. De voorspellingen werden gesteund door empirische data: vrouwelijke makaken A) vielen vaker individuen aan die hen tegenwerkten in een coalitie en ontvingen vaker tegenwerking van die dieren die hen sowieso vaker aanvielen en B) vlooiden vaker individuen van wie ze vaker tegenwerking in gevechten kregen en boden het vaakst tegenwerking tegen die dieren die hen het vaakst vlooiden. Omdat de patronen in het model het gevolg zijn van de ruimtelijke structuur, bevestigde de empirische data de suggestie dat bij echte primaten coalitie patronen ook een gevolg kunnen zijn van de ruimtelijke structuur van de groep.

In **hoofdstuk 5** heb ik het voorkomen van post-conflict affiliaties onderzocht tussen omstanders en eerdere tegenstanders van een gevecht in een empirische studie van de tonkeana makaak, *Macaca tonkeana,* en in het model. Hier heb ik voor het eerst het model gebruikt om een groep echte apen na te bootsen. De resultaten tonen aan dat patronen in post-conflict affiliaties hetzelfde waren voor het model als voor de empirische data. Het model suggereerde twee verschillende mechanismen voor het ontstaan van post-conflict affiliaties met omstanders: vermindering van angst en sociale

facilitatie. Sociale facilitatie was verantwoordelijk voor het ontstaan van post-conflict affiliaties met omstanders. In het model verhoogt sociale facilitatie de kans dat omstanders als eerst volgende aan de beurt komen na het gevecht. Bij echte dieren verhoogt een gevecht tussen twee individuen de opwinding van omstanders en dus de kans op interactie tussen omstanders en een van de eerdere tegenstanders na het gevecht. De vermindering van angst was de voornaamste drijfveer voor facilitatie van post-conflict affiliaties. Omdat een gevecht een stressvolle gebeurtenis is, zijn tegenstanders angstig na een conflict, een gegeven dat bevestigd wordt in empirische studies en geïmplementeerd is in het model. Oftewel, nadat een conflict over is, kunnen eerdere vechters proberen hun angst te verminderen door een omstander te vlooien. De mechanismen gesuggereerd door het model zijn eenvoudiger dan de mechanismen die tegenwoordig naar voren worden gebracht (zoals cognitive empathie) en dus verdienen ze het om in empirisch studies meer in detail onderzocht te worden.

Meer algemeen suggereert het model 'GrooFiWorld' een geïntegreerde theorie voor affiliatief en agressief gedrag bij primaten. De sleutel variabele hierbij is de intensiteit van agressie. De intensiteit van agressie bepaalt hoe steil een hiërarchie is en de ruimtelijke verdeling van individuen in de groep. Wanneer de intensiteit van agressie hoog is, lijken de patronen die ontstaan op de patronen die gevonden zijn in intolerante gemeenschappen: de hiërarchie is steil; individuen richten vlooien naar de hoger ge rangden in de hiërarchie en naar individuen van gelijke rang; agressie en tegenwerking in coalities zijn eenzijdig, dus een kant op gericht; er is weinig neiging tot verzoening en er wordt weinig tijd besteed aan vlooien en vechten; en vrouwtjes zijn nogal dominant relatief ten op zichte van de mannetjes. Deze patronen zijn omgekeerd wanneer de intensiteit van agressie laag is. Daarenboven, creëert de ruimtelijke locatie van individuen in de groep gedifferentieerde relaties die verantwoordelijk zijn voor het ontstaan van de wederkerigheid van vlooien en steunen, het

uitwisselen van vlooien voor steun en van steun voor vlooien, verzoening en verzoening met waardevolle partners. Opvallend is dat al deze gedragspatronen ontstaan zonder de aanname van hoog ontwikkelde cognitie. Dus, de resultaten verkregen in dit proefschrift wijzen erop dat het model 'GrooFiWorld' op zijn minst een aantal essentiële eigenschappen van echte primaten gemeenschappen weerspiegelt. Hopelijk zullen deze bevindingen empirici inspireren de mechanismen gesuggereerd door dit model te gaan onderzoeken.

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